HYDROGRAPHY AND MARINE PLANKTON OF TOLO HARBOUR, HONG KONG

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M.Phil. THESIS

DIVISION OF BIOLOGY
THE CHINESE UNIVERSITY OF HONG KONG

1991

Hydrography and marine plankton of Tolo Harbour, Hong Kong

by

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Thesis submitted in partial fufilment
of the requirements for the degree of
Master of Philosophy

June, 1991

Division of Biology
Graduate School
The Chinese University of Hong Kong

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Acknowledgements

I wish to express my gratitude to my supervisor, Dr. C.K. Wong for his instruction and guidance. I also thank him for his permission to use samples collected by him between November 1987 - May 1988. I am also very grateful to Dr. K.H. Chu and Dr. N.Y.S. Woo (Department of Biology, The Chinese University of Hong Kong) for their advice, criticism and support.

I would like to thank Professor W.G. Sprules (Department of Zoology, University of Toronto) for his willingness to serve as an External Examiner of this thesis.

I am also thankful to the staff at the Marine Science Laboratory, The Chinese University of Hong Kong, for their assistance and support throughout the period of this study. I am especially indebted to Mr. M.K. Cheung, Mr. K.C. Chung, Mr. G.C.K. Lau, Mr. Y.C. Tam and Miss K.P. Yeung for their assistance in the field and laboratory.

My special thank goes to my husband, Mr. N.P. Tam, for his endless support and encouragement during my study period.

Abstract

The hydrography and marine plankton of Tolo Harbour, Hong Kong, were studied at 4 stations between November 1987 and January 1990. Intense algal blooms, indicated by chlorophyll*a* concentrations >50 ng.mL^{-1}, were observed throughout the study period. Eutrophication was most pronounced in the inner harbour where water transparency was low and oxygen depletion in the bottom was severe.

The 5 most common genera of marine copepods were *Temora, Paracalanus, Acartia, Oithona*, and *Corycaeus*. The cyclopoid copepod *Oithona* was the most important zooplankter in Tolo Harbour in terms of abundance. It was followed by *Paracalanus, Acartia, Corycaeus*, and *Temora*. Two cladocerans, *Evadne* and *Penilia*, occurred in Tolo Harbour in about equal proportions.

Significant correlation was found between the abundance of crustacean zooplankton and temperature, but no obvious seasonal patterns could be identified. A dramatic decline in the abundance of marine zooplankton was observed in 1989. Deteriorating water quality, oxygen depletion in the bottom and increased domination of the phytoplankton by Dinophyceae are believed to be the major reasons for the decline.

The marine cladoceran *Penilia avirostris* occurred throughout the year, but the number was not related to temperature and the density was

never higher than 5 individuals.L^{-1}. Parthenogenetic females ranged from 0.3-1.0 mm in body length (BL) and 0.3-1.1 mm in gross length (GL). The number of parthenogenetic eggs or embryos varied from 1-13 per female, with a mean of 5.6. A significant positive relationship occurred between body length and brood size.

P. avirostris showed seasonal variations in body size and brood size. Individuals collected in summer were smaller than individuals collected during winter. Seasonal changes in body size might be related to predation pressure and food source limitation during summer.

Grazing behavior of *P. avirostris* was measured using the gut fluorescence technique. *P. avirostris* fed *Chaetoceros gracilis* and *Nannachloris oculata* in outdoor tanks showed pronounced diel variations in gut pigment content. Thus ingestion rates and clearance rates were higher at night than during daytime.

Feeding experiments were also performed using as food five strains of green algae and three strains of diatoms at concentrations ranging from 10 - 1800 ng Chl*a*. mL^{-1}. In general, gut content and ingestion rate increased with food concentration. Relationship between clearance rate and food concentration suggests two strategies in the feeding behavior of *P. avirostris*. Clearance rate either increased to a maximum value when food concentration approached zero or decreased to very low levels when food concentration dropped below a certain critical level.

The feeding impact of *P. avirostris* on the phytoplankton in Tolo Harbour was evaluated in June and November 1989. Feeding impact ranged from 0.01 - 31.56 mL of water swept clear.L^{-1}.day^{-1} in June when maximum chlorophyll*a* concentration in Tolo Harbour was 60.41 ng.mL^{-1}. During a red tide occurrence in November, feeding impact of *P. avirostris* captured in locations with chlorophyll*a* concentration > 50 ng.mL^{-1} was generally < 5.0 mL swept clear.L^{-1}.day^{-1}. This result suggests that the grazing impact of *P. avirostris* on the marine phytoplankton is low. Extremely low feeding impacts recorded during a red tide occurrence in November provide evidence that red tide organisms may adversely affect the feeding performance of *P. avirostris*.

Chapter 1

General introduction

Hong Kong, located on the southern coast of China and with a total land area of only 1,068 km^2, is one of most densely populated cities in the world. During the last 45 years, the population of Hong Kong increased from 600,000 in 1945 to about 6 million in 1990. To accommodate this growth, the Hong Kong Government has undertaken massive housing developments. An overwhelming proportion of the total population and factories is concentrated in the Kowloon Peninsula and along the northern coast of Hong Kong Island. Because of the asymmetrical urbanization, much of the sewage and industrial effluents enter the coastal waters through sewage outfalls and stormwater drains.

Pollution has been a major problem in urbanized areas of the New Territories since the early 1970's. Fishing and farming used to be the main occupations in the New Territories. In the 1960's, the Hong Kong Government decided that a significant proportion of the population increase should be in undeveloped areas of the New Territories. In the catchment of Tolo Harbour, population increased from a total of 73,000 in 1973 to about 500,000 in 1988 with development of the new satellite towns of Shatin and Tai Po. While there has been a steady decline in agricultural activities, discharge of sewage and industrial effluents is still causing a net overall increase in organic and nutrient loading in Tolo Harbour (Lam and Ho 1989). Two sewage treatment plants were commissioned in the early 1980's to provide secondary treatment for most of the human sewage from the new towns. Unfortunately, after the commissioning of the sewage treatment

plants, the discharge of pollution loads into Tolo Harbour was still exceeded the assimilative capacity of the waterbody, and the general water quality in Tolo Harbour was still found to be deteriorating.

Hodgkiss and Chan (1983) found that sedimentation and the absence of thorough mixing have resulted in the build-up of organic matters and nutrients in the bottom of Tolo Harbour. Cultural eutrophication, in turn, led to increases in algal growth (Holmes and Lam 1985). Indeed, the occurrence of algal blooms, red tides, red tide related oxygen depletion and fish kills have increased progressively since the late 1970's (Wu 1988).

This study attempts to examine the hydrography of Tolo Harbour. The aims are to evaluate the current conditions and to provide data for further comparative studies.

Regular water quality and phytoplankton monitoring have been undertaken in Tolo Harbour since 1977 (Hodgkiss and Chan 1983, 1987; Lam 1984; Wear *et al.* 1984; Holmes and Lam 1985; E.P.D. 1987, 1988, 1989, 1990; Lam and Ho 1989). Little, however, is known of the marine zooplankton in Tolo Harbour, and no major studies on the biology and ecology of the marine zooplankton have been carried out. Crustacean zooplankton forms an important component of most marine ecosystems. Zooplankton grazers constitute the major pathway for the transfer of energy between primary producers and organisms in the higher trophic levels. Because crustacean zooplankton forms the primary food for the early

life history stages of many commercially important fishes and marine organisms, information on their seasonal dynamics is of practical as well as scientific interest. A variety of physical and biological factors interact to affect the species composition and abundance of the zooplankton. Physical transport can substantially modify the abundance of zooplankton in bays and inlets (Lewis and Thomas 1986; Lindahl and Perissinotto 1987; Lindahl and Hernroth 1988; Aksnes *et al.* 1989). Abundance of zooplankton can be related to localized conditions of water temperature, salinity, food supply, and predation (Colebrook 1982, 1982a, 1985; Thomas and Emery 1986; Parsons and Kessler 1987). Thus a detailed survey of the hydrography, nutrient status and plankton abundance is clearly needed as a baseline against which the effects of increased pollution on the zooplankton community of Tolo Harbour could be assessed.

The cladoceran *Penilia avirostris* occurs most commonly in productive near- and in-shore environments of the subtropics and tropics (Pavlova 1959a; Della Croce and Venugopal 1973; Grahame 1976; Moore and Sander 1979). The association of *P. avirostris* with polluted bays and estuaries (Kiortsis and Moraitou-Apostolopoulou 1975; Grahame 1976; Moore and sander 1979) and with relatively productive nearshore waters suggests that *P. avirostris* may be an indicator of water pollution and eutrophication. Until recently, the biology and ecology of marine cladocerans have received very little attention. Although a number of researchers have described the distribution and abundance of *P. avirostris*, knowledge on the ecology and life history of these animals are relatively limited.

The major objective of this research is to study the relationship between the hydrograpy and marine zooplankton of Tolo Harbour. Chapter 3 presents the result of a hydrographical survey of Tolo Harbour. The impacts of eutrophication on nutrient status and phytoplankton dynamics are investigated. Chapter 4 documents the seasonal dynamics of major groups of marine zooplankton in Tolo Harbour. Chapter 5 presents some observations on the biology and ecology of *P. avirostris*. A more detailed study on the feeding behaviour of *P. avirostris* in Tolo Harbour is then presented in chapter 6.

Chapter 2

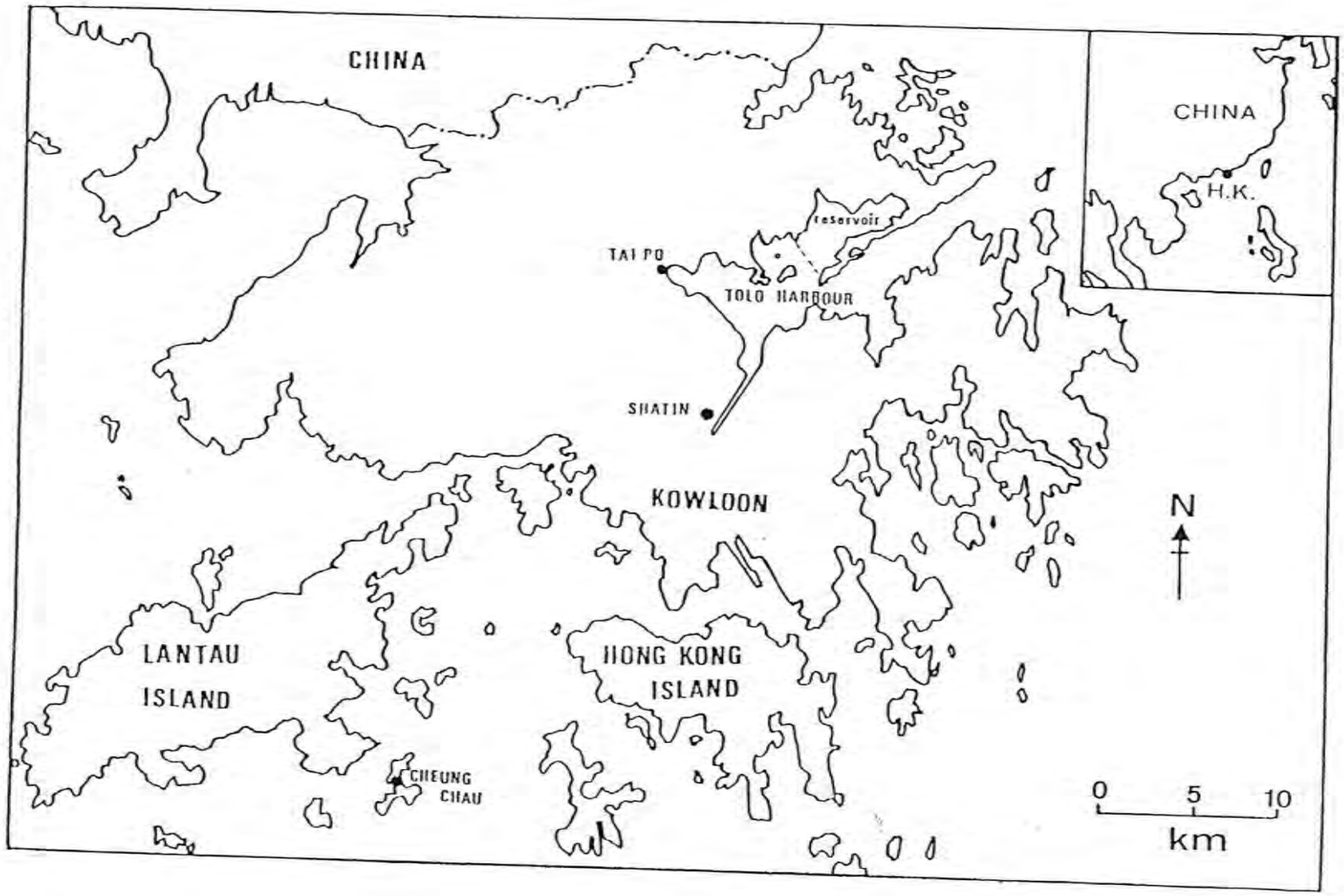
Literature review

2.1. The Tolo Harbour Water Control Zone

Tolo Harbour is a long, shallow and nearly land-locked waterbody located in the north-east of Hong Kong (Fig. 2.1). It is 16 km in length and, on average, 3 km wide. Mean water depth is about 12 m and maximum depth is 22 m. Total area is approximately 50 km^2. The outlet, which opens towards Mirs Bay, has a maximum width of only about 1.5 km. In 1967 a large cove inside the harbour was dammed off to become a freshwater reservior. Construction of the Plover Cove Reservoir and reclamations along the coast of the inner harbour for urban development have substantially altered the size and shape of the harbour. As a result, the volume of tidal exchange in the harbour was significantly reduced (Gordon 1975).

Because of the enclosed topography, the inlet has a restricted rate of tidal exchange. Average diurnal tidal difference in the inlet is 0.97 m, with mean high tide and mean low tide at 1.75 m and 0.78 m respectively (Hodgkiss and Chan 1983). Because prevailing north-easterly winds move only the near surface waters, average current velocity is 0.04 m/s in the inner harbour and increases progressively to about 0.08 m/s in the channel (Watson and Watson 1971). These current speeds are considerably slower than those recorded in Victoria Harbour and the North Western Waters Zone in Hong Kong (E.P.D. 1987). Oakley and Cripps (1972) reported low flushing rates in the inlet, with an average water residence time of about 35

Fig. 2.1. Tolo Harbour in its geographical setting.


CHINA
CHINA
H.K.
reservoir
TAI PO
TOLO HARBOUR
SHATIN
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LANTAU
ISLAND
HONG KONG
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10
km

days in the inner harbour. This indicates that most of the exogenous organic materials are likely to be decomposed and be recycled within the harbour.

Despite its limited waste receiving capacity, Tolo Harbour receives substantial pollutant loads from various sources. One important source is the large population in the catchment area. With development of the Shatin and Tai Po new towns, the catchment population increased from 73,000 in 1973 to 500,000 in 1989, and an ultimate figure of over 1 million is projected for the 1990's. The large catchment population has significantly increased the discharge of sewage into the harbour. Two sewage treatment plants were commissioned in 1982 to provide secondary treatment for most of the human sewage from the Shatin and Tai Po areas. A second important pollution source is the livestock rearing industry which has operated in the catchment for many years. Wastes produced by an estimated 10,000 pigs and 500,000 chickens are discharged directly into streams and flushed into the harbour (E.P.D. 1987). Other pollution sources include industrial discharges from factories, mainly in the Fo Tan area.

In order to improve the water quality of Tolo Harbour, the Hong Kong Government has introduced a number of pollution control strategies. The Tolo Harbour water control zone was gazetted in 1982 and specific water quality objectives were established. Effluent discharges from sewage treatment plants and specified industries in the catchment are monitored and controlled. In addition, the Livestock Waste Control Scheme was

implemented under the Waste Disposal Ordinance in June 1988. Rearing of livestock in Shatin and part of Tai Po is largely prohibited. Unfortunately, even though there has been a steady decline in agricultural activities, sewage discharge from the expanding human population has still caused a net overall increase in organic and nutrient loads into Tolo Harbour (Lam and Ho 1989).

Many authors (Trott 1972; Trott and Fung 1973; Kueh 1974; Wong *et al.* 1977; Thompson and Ho 1981; Hodgkiss and Chan 1983, 1987; Wear *et al.* 1984; Chan and Hodgkiss 1987) have reported on the deteriorating water quality in Tolo Harbour. In general, there has been a progressive increase in the concentrations of nutrients, chlorophyll*a*, red tide organisms, and waterborne pathogens. No improvement in water quality has been recorded since the commissioning of the sewage treatment plants and the establishment of the Tolo Harbour water control zone. The steady and progressive decline in dissolved oxygen level is continuing and the occurrence of fish kills due to red tides and oxygen depletion has become a regular phenomenon.

2.2. Hydrography of Tolo Harbour

The hydrography of Tolo Harbour is affected by factors such as local stream run-off, coastline configuration and topography. Because current flow in inner Tolo Harbour is restricted, turbulent mixing of the

water column is limited. One result of poor mixing is that water temperature in the surface is high and stratification of the water column in the summer is intense.

2.2.1. Temperature

The surface seawater temperature of Tolo Harbour reflects the seasonal variation in air temperature (Wear *et al.* 1984). The general trend is that water temperature is highest in the summer and lowest in the winter. In 1972 the overall mean surface temperature was 32.3^{o}C for the summer and 11.6^{o}C for the winter (Trott and Fung 1973). However, in another survey in 1976 mean surface temperature was found to vary from 31^{o}C in the summer to 14^{o}C in the winter (Wear *et al.* 1984). Similar results were recorded in 1978 when summer and winter temperatures were 30.5^{o}C and 15^{o}C respectively (Hodgkiss and Chan 1983). Thus the seasonal temperature ranges recorded in 1976 and 1978 were somewhat narrower than that recorded earlier by Trott and Fung in 1973. Since mean air temperature recorded in the 1976 and 1978 studies did not differ significantly from that recorded by Trott and Fung (1973), the reduced range of water temperature was probably not caused by changes in air temperature. It seems likely that the narrower temperature range reflects a stenothermal state in Tolo Harbour which is related to changes in harbour configuration caused by extensive reclamation and increases in turbidity.

2.2.2. Salinity

Average salinity of fresh water varies between 0.065 ppt and 0.3 ppt, while the open sea generally has salinity ranges from 33 ppt to 38 ppt (Reid and Wood 1976). Surface water in Tolo Harbour is generally more saline in winter and spring than in the summer and early autumn rainy season when fresh water run-off was at its maximum. Kueh (1974) reported that mean salinity in Tolo Harbour for 1973, with the normal 1466 mm of rain between June and August, was 25.6 ppt in summer and autumn, and 31.7 ppt in winter and spring. In 1974 when total rainfall between June and August was much lower (305 mm), mean salinity during summer and autumn was 28.9 ppt (Kueh 1974). When typhoon 'Carmen' brought in 474 mm of rainfall over a three-day period in October 1974, salinity of surface water dropped to about 18.6 ppt. Because Tolo Channel is closer to the open sea, salinity is higher and more stable than in the inner harbour.

Surface water in Tolo Harbour is diluted by freshwater from streams. Trott (1973) reported that the salinities of Tolo Harbour ranged from 24.5 to 33.5 ppt in the surface, and from 29 and 33 ppt in the bottom. Very similar values of 24 to 33 ppt for surface and 29 to 34 ppt for bottom were reported by Hodgkiss and Chan (1983). The vertical salinity gradient is magnified aften monsoon rains when surface water over the entire area of Tolo Harbour shows significant reductions in salinity, whereas the bottom water remains virtually unaffected.

2.2.3. Secchi depth

The transparency and light penetration characteristics of seawater are affected by the presence of suspended particles such as clay, silt, finely divided organic and inorganic matters, plankton and other microscopic organisms. Parameters which are commonly used to indicate these properties include Secchi depth, turbidity and suspended solids content.

The transparency of sea water can be determined by making visual observations on a submerged black and white Secchi disc. Water depth at which the Secchi disc disappears from view is measured as the Secchi depth. The greater the Secchi depth, the higher the transparency of the surface water layer.

No distinct seasonal patterns of variation in water transparency have been observed in Tolo Harbour. The observations reveal, however, that there has been a general decrease in Secchi depth, ranging from 8.3 m in Tolo Channel to 2.1 m in Tai Po Hoi (Kueh 1974). In 1975 Secchi depth ranged from 5-10 m in the channel to about 5 m in the harbour (Wear *et al.* 1984). Several years later in 1978 Hodgkiss and Chan (1983) observed that the average Secchi depth had decreased to 2.44 m in the inner parts of the harbour and 5.67 m in the mouth region of the channel. Those observations suggest that sewage pollution had already impacted the water quality of Tolo Harbour between 1975 and 1978.

2.2.4. Dissolved oxygen

When organic matter is discharged into marine water, a substantial portion of it is decomposed. During decomposition, oxygen is consumed by bacterial respiration and dissolved oxygen content of the water is lowered. Hence the level of dissolved oxygen to some extent reflects the level of organic pollution in the water. In contrast to oxygen depletion, supersaturation of oxygen (annual median greater than 100% saturation) caused by the active growth of algae which produces oxygen during photosynthesis, indicates eutrophication. Supersaturation of oxygen has been detected in the surface water of Tolo Harbour and Channel (Wear *et al.* 1984). While active algal growth may increase oxygen content in surface water, oxygen depletion in the bottom occurs during the decomposition of sedimenting algal materials. Oxygen supersaturation therefore implies an environmental problem.

Like temperature and salinity, dissolved oxygen levels in Tolo Harbour exhibit seasonal changes. In early summer (April to May), oxygen levels in the bottom fall due to high oxygen demand from bacterial respiration in decomposition of organic matters in the sediment at warmer temperature. At the same time oxygen level in the surface rose as a result of active algal growth. These changes produce a strong vertical gradient in dissolved oxygen level. The gradient persists during the summer because vertical mixing is largely prevented by temperature and salinity stratification

in the water column. With the commencement of winter in October and the disappearance of thermocline, strong northeast monsoon induces better turbulent mixing in the water column. At such time, the oxygen stratification in the water column disappears.

Kueh (1974) reported that, in 1973, the mean seasonal value of dissolved oxygen in the surface water, expressed in percent saturation, was highest in the channel and decreased progressively toward the inner harbour. The overall mean values for Tolo Channel and Tolo Harbour were 95.9% and 95.6% saturation respectively. No distinct seasonal pattern of dissolved oxygen was observed. In another survey conducted in 1975, Wear *et al.* (1984) found that although the level of dissolved oxygen in the surface water had increased to about 100 % saturation, dissolved oxygen levels in the bottom showed a significant decrease. In that survey the lowest value of 24.7% saturation was recorded in the inner Harbour in September. At the same time a slightly higher value of 37.7% saturation was recorded at Mirs Bay. In both 1974 and 1975, dissolved oxygen concentrations in bottom water increased after the disappearance of the thermocline, and remained high throughout the winter.

2.3. Eutrophication in Tolo Harbour

Many areas of coastal waters in Hong Kong receive sewage directly from urbanized catchment, as well as waste discharges from domestic,

livestock and industrial sources via streams and stormwater run-off. Most of these waste discharges carry heavy loads of nitrogen and phosphorus which stimulate phytoplankton growth.

In an eutrophic waterbody, intense growth of phytoplankton may upset the ecological balance and exert adverse impacts on water quality. Decline of algal blooms is followed by the decomposition of algae by bacteria in the sediment. Bacterial respiration consumes oxygen and the bottom water may become anoxic. In Tolo Harbour, oxygen depletion has been implicated in numerous occurrences of mass mortality of fish and benthic organisms (Wu and Richards 1979; Horikoshi and Thompson 1980; Wu 1982). Fish kills at various mariculture zones in Tolo Harbour have resulted in great economic loss. Under anoxic conditions, hydrogen sulphide, a foul smelling toxic gas, is emitted, rendering the environment unpleasant and constituting a public health hazard. The marked increase in the occurrence of red tide since the 1970's is accompanied by an alarming increase in the diversity of causative species (Holmes and Lam 1985; Lam and Ho 1989). In the case of toxic red tides, not only fish kills occur, there was the added risk of food poisoning when people consume contaminated seafood.

2.3.1. Nutrients

Nitrogen and phosphorus are the major nutrients required for phytoplankton growth. Human sewage and livestock wastes contain large

quantities of nitrogen and phosphorus compounds in various forms. Inorganic forms which are most readily available to plants are the major elements responsible for eutrophication.

Nitrite nitrogen occurs in very minute quantities in unpolluted waters and nitrate nitrogen also tends to occur only in relatively low levels (around 0.3 $\mu g.L^{-1}$). For this reason the presence of nitrite and nitrate nitrogen in greater concentrations is often used as evidence of organic pollution. Normally, nitrite nitrogen is produced in natural waters as a result of oxidation of nitrogenous organic compounds by nitrifying bacteria, and also as a result of reduction of nitrates. Reid and Wood (1976) suggest that the latter process is the more important one, particularly where oxygen levels are well below saturation.

Nitrogen concentration in the water of Tolo Harbour shows no clear seasonal periodicity and fluctuates unpredictably throughout the year. According to result of a 1978 survey (Hodgkiss and Chan 1983), NO_2-N concentration in the inner Harbour ranged from 13.6 $\mu g.L^{-1}$ to 15.7 $\mu g.L^{-1}$ in surface water and 14.7 $\mu g.L^{-1}$ to 16.2 $\mu g.L^{-1}$ in bottom water. Mean values for Tolo Channel were comparatively lower at 9.7 $\mu g.L^{-1}$ in the surface and 8.2 $\mu g.L^{-1}$ in the bottom.

Stirling and Wormald (1977) found that the highest PO_4-P level was 37 $\mu g.L^{-1}$ recorded near Tai Po Hoi. Several years later Hodgkiss and Chan (1983) confirmed that the highest level at Tai Po Hoi was at around 44 $\mu g.L^{-1}$, but in mid harbour and Tolo Channel much higher values of 204

$\mu g.L^{-1}$ and 326 $\mu g.L^{-1}$ were recorded. These values show a clear increasing trend in nutrient level.

Stirling and Wormald (1977) suggested that because of adsorption reaction in sediments, annual mean concentration of PO_4-P in the water of Tolo Harbour should be as low as 3 - 9 $\mu g.L^{-1}$. Thus although PO_4-P will accumulate in the sediments, addition of phosphate to the water may not necessarily lead to eutrophication of the water column. However, Hodgkkiss and Chan (1983) found that the annual mean concentrations of PO_4-P in Tolo Harbour were 9.2 $\mu g.L^{-1}$ for surface waters and 18 $\mu g.L^{-1}$ for bottom waters. These observations suggest that the input of phosphorus into Tolo Harbour has exceeded the buffering capacity of the sediments. Value for bottom waters in particular was above the limit of 15 $\mu g.L^{-1}$ considered necessary for the establishment of large algal blooms (Wilson and Dickson 1977).

As a result of land-locked topography and slow tidal circulation (Watson and Watson 1971), residence time for water in Tolo Harbour is long. Preston (1975) reported residence times of 23 days for Tai Po Hoi and 16 days for the central part of harbour. In addition, prevailing north-easterly winds moving the near surface water landward tend to prevent rapid removal of less saline and thus less dense terrestrial run-off. Oakley and Cripps (1972) pointed out that terrestrial run-off contributes much polluted water to Tolo Harbour and it takes about 35 days for terrestrial run-off to wither away. Thus, removal of waste materials from the harbour is impeded

and accumulation results. Sedimentation and absence of thorough mixing in turn cause nutrient accumulation to take place at the bottom of Tolo Harbour. The development of anoxic conditions following phosphate accumulation (Pierrou 1975) has been documented in Tolo Harbour, particularly in Shatin Hoi and Tai Po Hoi (Preston 1975). Hodgkiss and Chan (1987) reported a fivefold increase in dissolved inorganic nitrogen level and a tenfold increase in dissolved inorganic phosphorus level from 1978 to 1985 in the surface water of Tai Po Hoi. It is likely that, with increased nutrient loading as a result of sewage discharges from the rapidly developing new towns, water conditions in Tolo Harbour will deteriorate further.

2.3.2. Chlorophyll*a*

Chlorophyll*a* level in seawater provides an indirect estimate of phytoplankton biomass in the water (Kleppel 1988). In general, mean chlorophyll*a* levels above 10 $ng.mL^{-1}$ is regarded as unacceptably high and as a sign of eutrophication (E.P.D. 1987). In natural off-shore oceanic waters the chlorophyll*a* levels are generally below 2 $ng.mL^{-1}$ (E.P.D. 1987). For comparison, annual mean chlorophyll*a* concentration in the surface waters of Tolo Harbour is higher than 10 $ng.mL^{-1}$ (E.P.D. 1990)

As early as 1975 Wear *et al.* (1984) reported high chlorophyll *a* concentrations in waters close to Plover Cove. A single peak of 13500 $ng.mL^{-1}$ was recorded in August, although concentration during the rest of the year was always lower than 10 $ng.mL^{-1}$. Considerably higher

concentrations were reported by Chan and Hodgkiss (1987) several years later. In waters close to the Tai Po Sewage Treatment Plant, mean concentrations of 14.36 $ng.mL^{-1}$ and 17.12 $ng.mL^{-1}$ were recorded in 1983 and 1984 respectively. In the channel where nutrient levels were lower, mean chlorophyll*a* concentrations were 2.69 $ng.mL^{-1}$ in 1983 and 4.12 $ng.mL^{-1}$ in 1984.

Tolo Harbour represents an example of eutrophication which has proceeded at a very fast rate (E.P.D. 1987). In addition to the long existing problem of livestock wastes from stream discharges, input of secondarily treated sewage effluents from the expanding population provides large quantities of inorganic nutrients for algal growth. The number of red tide occurrences has been on the increase since the 1970's (E.P.D. 1988). The topography of Tolo Harbour, which results in slow current movements, provides a stable environment for algal blooms to develop. In fact low nutrient levels sometimes measured in Tolo Harbour (E.P.D. 1987) indicate that dissolved nutrients are in a continuous flux due to vigorous growth of phytoplankton. After intensive uptake of nutrients by phytoplankton, levels measured in the water may be very low. Nutrient levels therefore may not always reflect the eutrophication problem.

2.3.3. Red Tides

Algal blooms in marine environments are generally caused by vigorous growth of diatoms and dinoflagellates. When a bloom is dominated

by dinoflagellates, the sea turns pink, orange, red or brown, depending on the organisms involved. This discolouration of the sea surface is referred to as a red tide.

Red tides can affect large areas of the sea and, once they have occurred, are very difficult to control. Apart from being unsightly, red tides can cause mass mortality of marine organisms. During the decline of a bloom, large amount of oxygen is taken up from the water, causing oxygen depletion and death of marine organisms. Some dinoflagellates are toxic. Toxins produced by some species can kill many fish directly. While many shellfish are unaffected, they accumulate the toxins even from very low concentrations of dinoflagellates (Halstead and Schantz 1984). The toxins stay in the shellfish for a very long time (Holmes and Lam 1985). Because of biological amplification, human consumption of fish and shellfish from areas affected by toxic red tides poses the risk of seafood poisoning which can be fatal. Toxins associated with dinoflagellates have been known to cause many kinds of seafood poisoning including DSP (diarrhetic shellfish poisoning), PSP (paralytic shellfish poisoning), NSP (neurotoxic shellfish poisoning) and ciguatera fish poisoning (Quayle 1969; Prakash *et al.* 1971; Shimizu 1983; Holmes and Lam 1985).

Red tide occurrences in Hong Kong have been on the increase since the 1980s (E.P.D. 1988). Tolo Harbour accounts for approximately over half of the red tide occurrences in Hong Kong each year. While red tide blooms in unpolluted waters are probably natural phenomena, incidences in semi-enclosed waterbodies such as Tolo Harbour is often closely related to

eutrophication. In 1987 the total number of red tide occurrences recorded for all coastal waters in Hong Kong was 33, with 17 happened in Tolo Harbour (E.P.D. 1988). The major causative organisms included *Noctiluca scintillans, Prorocentrum triestinum, Peridinium faeroense, Crytomonas* spp. and a range of small flagellates (Holmes and Lam 1985). *Skeletonema costatum,* a diatom, have also caused discolouration of seawater by imposing a greenish brown colour (E.P.D. 1988, 1989).

In 1988 the Environmental Protection Department of Hong Kong (1989) reported in Tolo Harbour a continuous red tide caused by the dinoflagellate, *Gonyaulax polygramme*. The bloom lasted three and a half months from early February to mid-May. At the height of the bloom, cell concentration of *G. polygramme* reached 23,000 cells.mL^{-1} and surface water in most parts of the harbour appeared reddish brown. When the red tide gradually declined in early May, an extensive area of Tolo Harbour was covered with floating scum. An unpleasant odor was also detected along the shores of the inner harbour due to decay of dead organisms. A second species, *S. costatum*, became dominant towards the end of April, reaching concentrations of up to 40,000 cells.mL^{-1}. By the end of 1988, a total of 39 red tide ocurrences was recorded in Tolo Harbour.

2.4. Marine plankton in Tolo Harbour

2.4.1. Phytoplankton

Diatoms and dinoflagellates are the two major components of marine phytoplankton. Members of diatom typically dominate the marine phytoplankton in unpolluted marine waters. However, dinoflagellates, which contain orange and red pigments besides chlorophyll, sometimes undergo short- term population explosions in response to local conditions. Some of the fast growing dinoflagellates cause the red tides observed in coastal waters.

The species composition of the marine phytoplankton in Tolo Harbour was studied comprehensively by Hodgkiss and Chan (1987). Thirty-two genera and eighty-three species of Bacillariophyceae were recorded from inner Tolo Harbour. The 5 dominant forms were *Skeletonema costatum, Stephanopyxis turris, Rhizosolenia indica, Thalassiosira condensata* and *Thallossiothrix frauenfeldii*. Only 14 genera and 60 species of Dinophyceae occurred in the region. Dominant forms included *Prorocentrum micans, Prorocentrum gracile, Protoperidinium minutum, Gymnodinium mikimotoi* and *Gymnodinium splendens*. In the channel Bacillariophyceae comprised 36 genera and 128 species of which *Nitzchia pacifica, Skeletonema costatum, Rhizosolenia gracillima, Chaetoceros eibenii* and *Thalassiothrix frauenfeldii* were dominant. Dinophyceae contributed 13

genera and 60 species to the phytoplankton in the channel, with *Prorocentrum micans, Gymnodinium splendens, Ceratium furca, Prorocentrum triestinum* and *Dinophysis homunculus* constituting the most dominant forms.

2.4.2. Zooplankton

Zooplankton is the animal portion of the plankton community. The group includes the larval stages of some commercially important fish species and almost every major invertebrate phylum (Chen 1982). But the most important one in terms of number and biomass are crustaceans, principally copepods and cladocerans.

The zooplankton in the marine environments of Hong Kong was recently surveyed by Chen (1982). In most areas the zooplankton was dominated by copepods and cladocerans. A total of 52 species of copepods including 37 Calanoida, 13 Cyclopoida and 2 Harpacticoida were found. These were distributed among 19 families with the most important being the Paracalanidae, Calanidae, Eucalanidae, Acartiidae, Temoridae, Euchaetidae, Pontellidae, Oithonidae, and Corycaeidae. On average copepods constituted between 2-70% of the marine zooplankton. In comparison, cladocerans comprised less than 1% of the zooplankton community. In the surface waters, however, they sometimes formed one of the major faunal components. Only two species, *Penilia avirotris* and

Evadne tergestina, were reported.

Chapter 3

The hydrography and marine plankton of Tolo Harbour

3.1. Introduction

Since the mid-1970's urban development around Tolo Harbour has proceeded rapidly. The population increased from 73,000 in 1973 to more than 500,000 in 1989, and a figure of over 1 million is projected for the 1990's. While there has been a steady decline in agricultural activities, sewage discharge from the expanding population is still causing a net overall increase in organic and nutrient loading (Lam and Ho 1989). Two sewage treatment plants were commissioned in the early 1980's to provide secondary treatment for most of the human sewage from the new towns of Shatin and Tai Po, but this has not reduced the risk of eutrophication from increased nutrients input.

Many investigators (Trott and Fung 1973; Hodgkiss and Chan 1983; Wear *et al.* 1984) have reported on the deteriorating water quality in Tolo Harbour. In general there has been a dramatic increase in nutrient concentration in the entire water column and a gradual decrease in dissolved oxygen level in the bottom waters. Hodgkiss and Chan (1987) reported a tenfold increase in dissolved inorganic phosphorus concentration and a fivefold increase in dissolved inorganic nitrogen concentration from 1978 to 1985 in the surface water of Tai Po Hoi. Because of the well established thermocline and halocline in Tolo Harbour, anoxia of bottom waters is common in the summer. Very low (24.7% saturation) dissolved oxygen levels were measured in the bottom waters in 1975, before eutrophication

became a serious problem (Wear *et al.* 1984). Since then a trend of gradual decrease in dissolved oxygen level has developed (E.P.D. 1989).

Increase in nutrient loading and decrease in dissolved oxygen level have imposed considerable stress upon the biological communities. Increases in abundance of phytoplankton and dominance of dinoflagellates have been related to increasing nutrient levels in Tolo Harbour (Wear *et al.* 1984; Chan and Hodgkiss 1987; Hodgkiss and Chan 1987; Lam and Ho 1989). During the 1980's oxygen depletion in the summer has been implicated in periodic large scale fishkills at various mariculture sites (Holmes and Lam 1985). At the same time, the abundance, biomass and species diversity of fish in Tolo Harbour and Tolo Channel have shown steady decline (Wu 1988). Several recordings of mass mortality of benthic organisms have also been attributed to summer depletion of oxygen (Wu and Richards 1979; Horikoshi and Thompson 1980; Wu 1982).

Despite regular monitoring of water quality and phytoplankton, relatively little attention has been given to the marine zooplankton in Tolo Harbour. Chen (1982) reported that micro-crustaceans such as copepods and cladocerans are the most important zooplankters in the shallow coastal waters of Hong Kong in terms of abundance and diversity. A more recent survey by Wear *et al.* (1984) provided information on zooplankton biomass in Tolo Harbour, yet no investigation on the relationship between eutrophication and zooplankton dynamics has been carried out. Information on zooplankters is important because they are major

components of the marine food web and changes in their abundance and species composition may ultimately affect the trophic structure. A detailed survey was initiated in 1987 to study the impacts of hydrography and eutrophication on the abundance, composition, seasonal dynamics and spatial distribution of the marine zooplankton in Tolo Harbour. Part of the results are presented in this chapter.

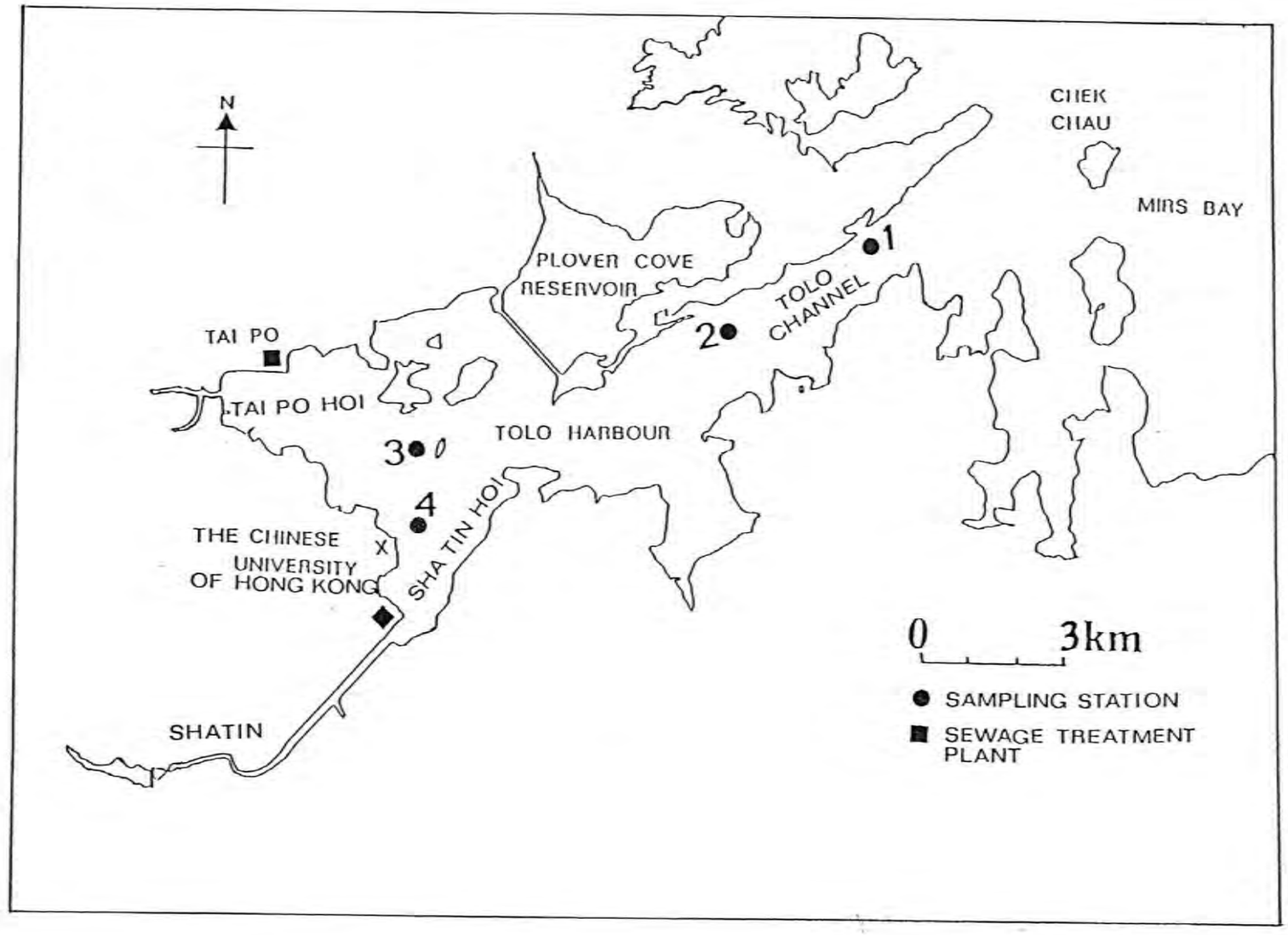
3.2. Materials and Methods

Hydrography and marine plankton were studied at 4 stations (Fig. 3.1) at roughly monthly intervals from November 1987 to January 1990, but analyses for chlorophyll did not begin until May 1988 and nutrient concentrations was measured twice on January and June 1990. All measurements and samplings were done between 0900 h and 1300 h.

Water temperature and dissolved oxygen in the surface and bottom were measured *in situ* with an electronic oxygen meter (YSI Model 57). Salinity of surface water was determined by a refractometer. Water transparency was estimated with a 30 cm diameter Secchi disc.

Zooplankton was sampled by making duplicated vertical hauls from bottom to surface with a conical net of 50 cm mouth diameter and 0.125 mm mesh size. The contents of each net haul were concentrated in 100 mL of filtered (0.125 mm) seawater and preserved immediately in 4% formaldehyde. In the laboratory, densities of crustacean zooplankton were estimated by counting subsamples under a stereomicroscope. Identification of crustacean zooplankton was base on the taxonomic guide of Cheng *et al.* (1988). At least two 3 mL subsamples were counted for each sample. For dry weight determination, a 50 mL subsample of each sample was rinsed with distilled water and dried to constant weight at 60 ^{o}C.

Fig. 3.1 Map of Tolo Harbour showing location of sampling stations.


N
CHEK CHAU
MIRS BAY
PLOVER COVE RESERVOIR
TOLO CHANNEL
1
2
TAI PO
TAI PO HOI
TOLO HARBOUR
3
4
THE CHINESE UNIVERSITY OF HONG KONG
SHA TIN HOI
SHATIN
0 3km
SAMPLING STATION
SEWAGE TREATMENT PLANT

At each station, seawater samples were collected 1 m below the surface with a Van Dorn water sampler. Two subsamples of 500 mL each were preserved immediately in Lugol's iodine for phytoplankton identification and counting. A third 500 mL subsample was stored in a dark polyethylene bottle for chlorophyll*a* analysis. In the laboratory, phytoplankton samples were allowed to settle in glass cylinders. Aliquots of condensed samples were transferred to a Sedgewick Rafter counting chamber and examined under an inverted microscope. For measurement of chlorophyll*a* concentrations, aliquots of 1 or 2 mL were filtered with 0.45-μm Millipore filters. The filters were extracted for at least 5 h in 90% aqueous acetone. Chlorophyll*a* concentration of extracted samples was measured with a Turner Model-112 fluorometer (Parsons *et al.* 1984).

Water samples for determination of nutrient concentration were collected from the surface with a bucket, stored in dark polyethylene bottles and kept frozen for subsequent analysis. Dissolved inorganic nitrogen (nitrate and nitrite) and phosphate were analysed according to methods described by Parsons *et al.* (1984).

3.3. Results

Seawater temperature in Tolo Harbour ranged from 15°C in March 1988 to 33°C in September 1989 (Fig. 3.2). Water temperature in the winter was typically around 15- 19°C. Gradual warming of the water column began in March and a thermocline appeared at all stations at the beginning of May. Summer temperatures ranged between 27-31°C at the surface and fell to between 17-29°C at the bottom. Water temperature began to drop after September. Thermoclines at all stations started to break down in November when seawater temperature at the surface fell to around 26°C.

Levels of dissolved oxygen in the seawater fluctuated considerably throughout the study period, although no clear trend of spatial variation was observed (Fig. 3.3). Differences between surface and bottom waters were greatest in the summer. Surface waters of the entire area of Tolo Harbour and Tolo Channel were supersaturated with dissolved oxygen. In contrast, much lower levels of dissolved oxygen were measured in the bottom waters. Oxygen depletion was particularly serious during the summer of 1988 when bottom dissolved oxygen fell to $< 10\%$ saturation at all stations. Oxygen depletion in the bottom waters was detected again at stations 1 and 2 during the summer of 1989, but bottom waters at the shallower stations 3

Fig. 3.2 Depth-time diagram of isotherms (^{o}C) at the 4 stations in Tolo Harbour.

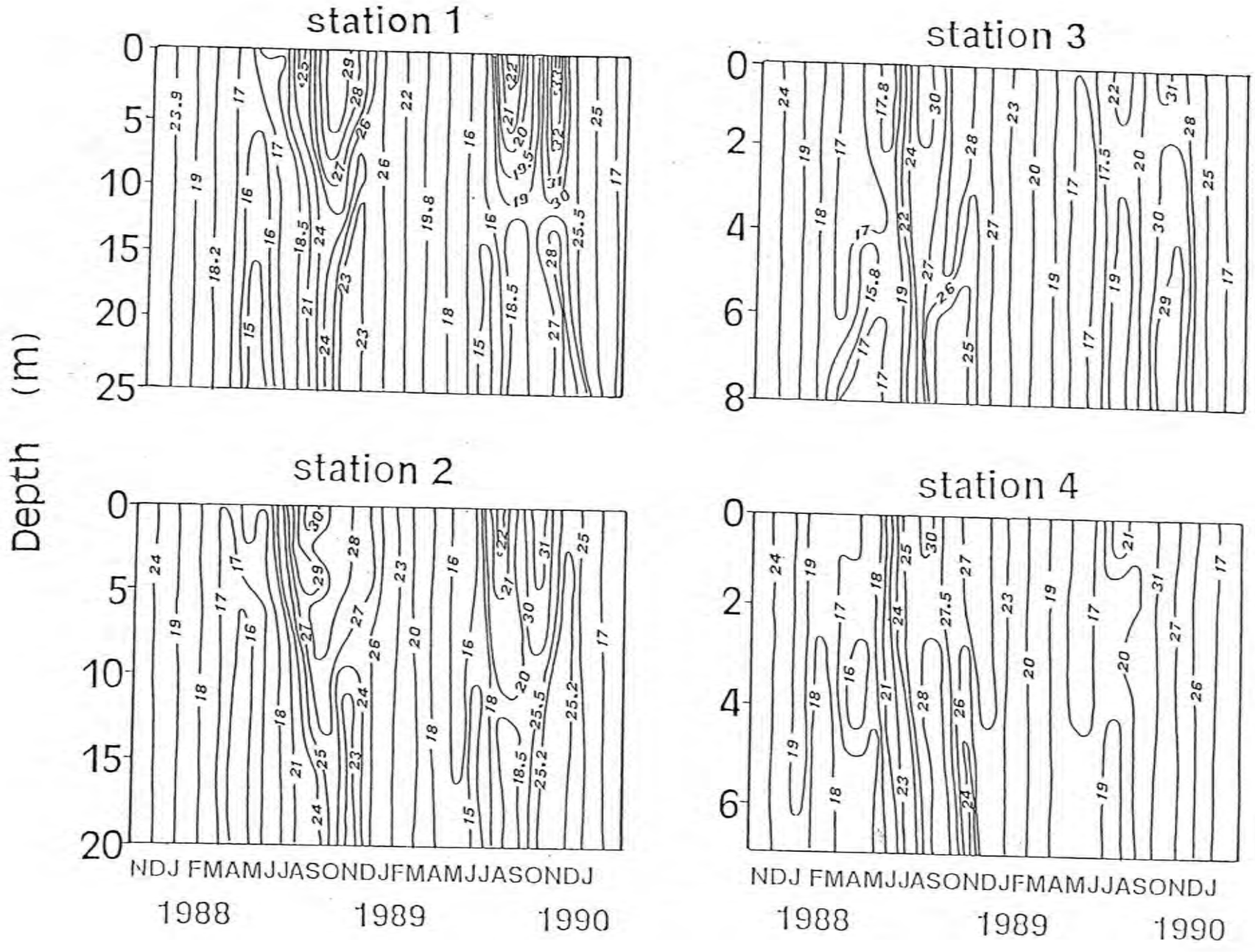
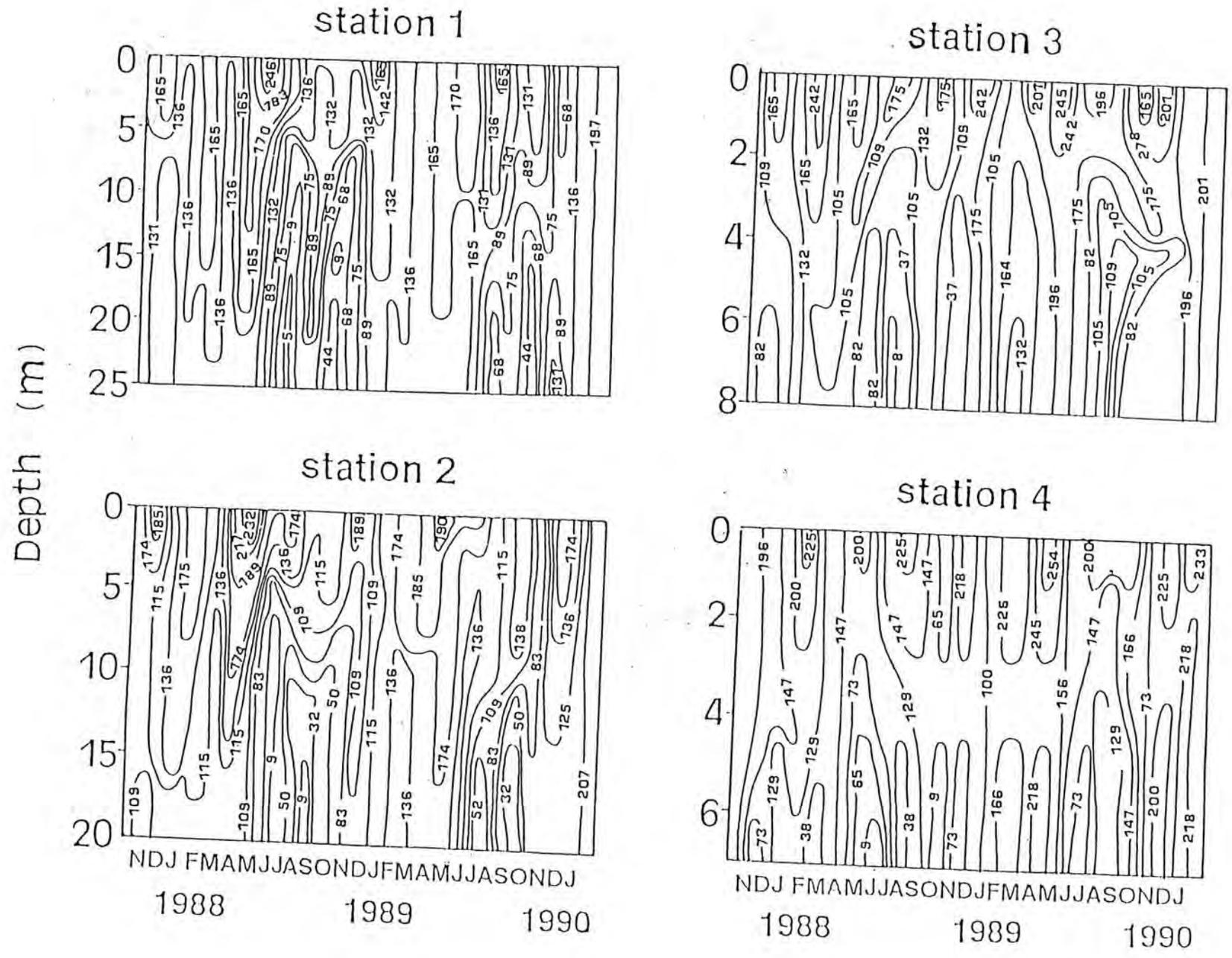

station 1
station 3
station 2
station 4
Depth (m)
0
5
10
15
20
25
2
4
6
8
NDJ FMAMJJASONDJFMAMJJASONDJ
1988
1989
1990

Fig. 3.3 Depth-time diagram of isopleths of dissolved oxygen concentrations in percentage oxygen saturation at stations 1-4.


station 1
station 3
station 2
station 4
Depth (m)
0
5
10
15
20
25
2
4
6
8
NDJ FMAMJJASONDJFMAMJJASONDJ
1988
1989
1990

and 4 remained relatively saturated with oxygen (> 100% saturation).

Salinity of surface water varied from the highest value of 38 ppt at station 1 in June 1989 to the lowest value of 30 ppt at station 4 in August 1988 (Fig. 3.4). In general, there was a gradual decrease in salinity from stations in Tolo Channel to stations in Tolo Harbour.

Spatial and temporal variations in Secchi depth were large (Fig. 3.5). At station 1, the outermost station, values were usually around 6 m. On the other hand, values at stations 3 and 4, the two inner stations, never exceeded 4 m. The highest value of 12.5 m was observed at station 1 in January 1989 and the lowest value of 0.75 m was observed in November 1988 at the same station. Temporal variations in Secchi depth were much higher at stations 1 and 2 than at stations 3 and 4.

Nutrient concentrations in January and June 1990 showed a marked decrease from the inner harbour to the channel (Fig. 3.6). Levels of dissolved inorganic phosphate varied from 73.3-108.8 $\mu g.L^{-1}$ at stations 3 and 4 to 38.9-46.5 $\mu g.L^{-1}$ at stations 1 and 2. Similarly, levels of inorganic nitrogen varied from 126.5-247.1 $\mu g.L^{-1}$ at stations 3 and 4 to 35.4-35.5 $\mu g.L^{-1}$ at stations 1 and 2.

Variation in chlorophyll*a* concentration among stations was high (Fig. 3.7). Mean values at stations 3 and 4 over the study period were 49.4

Fig. 3.4 Surface salinity at 4 stations in Tolo Harbour.

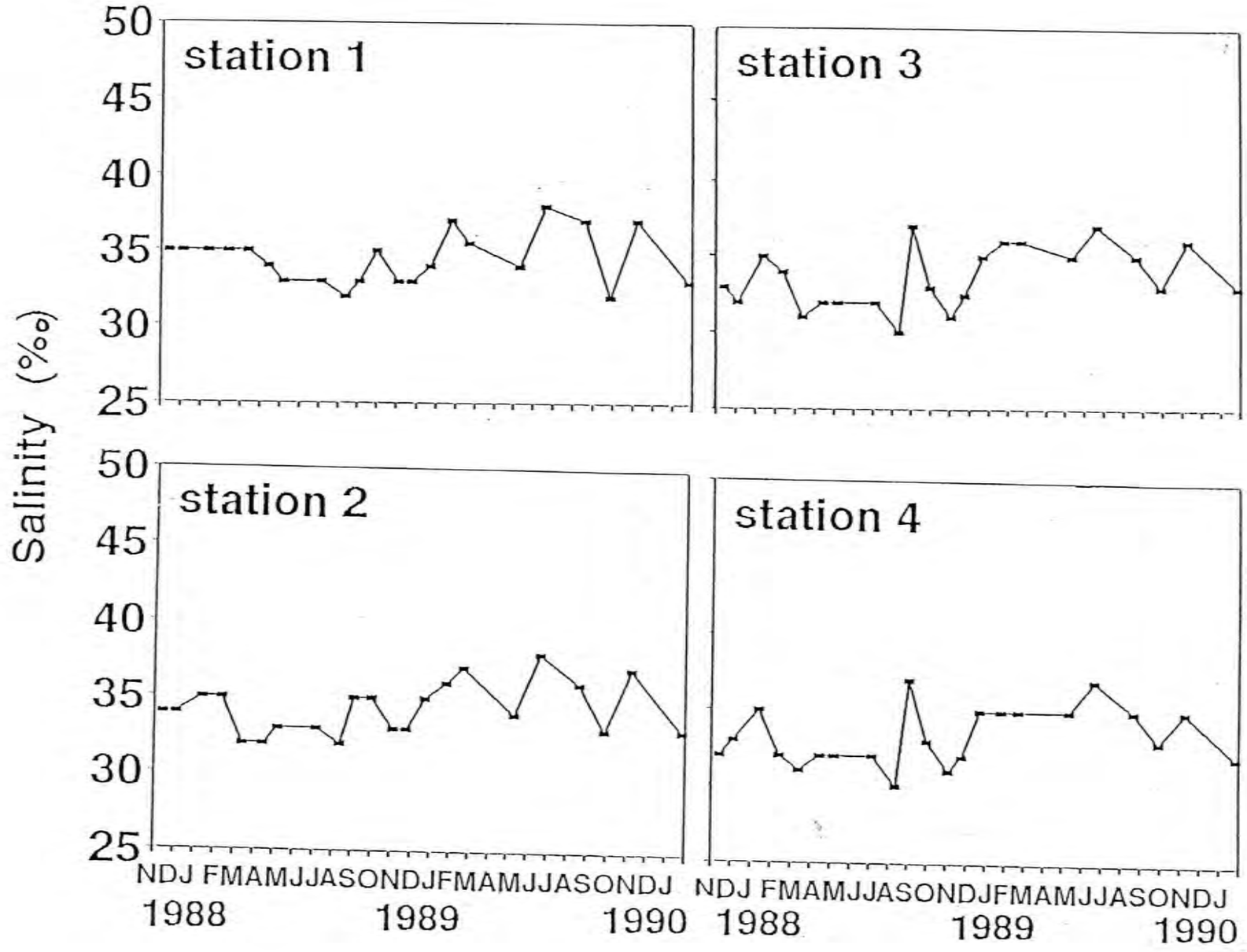

station 1
station 3
station 2
station 4
Salinity (‰)
50
45
40
35
30
25
NDJ FMAMJJASONDJFMAMJJASONDJ
1988
1989
1990

Fig. 3.5 Secchi depth at 4 stations in Tolo Harbour.

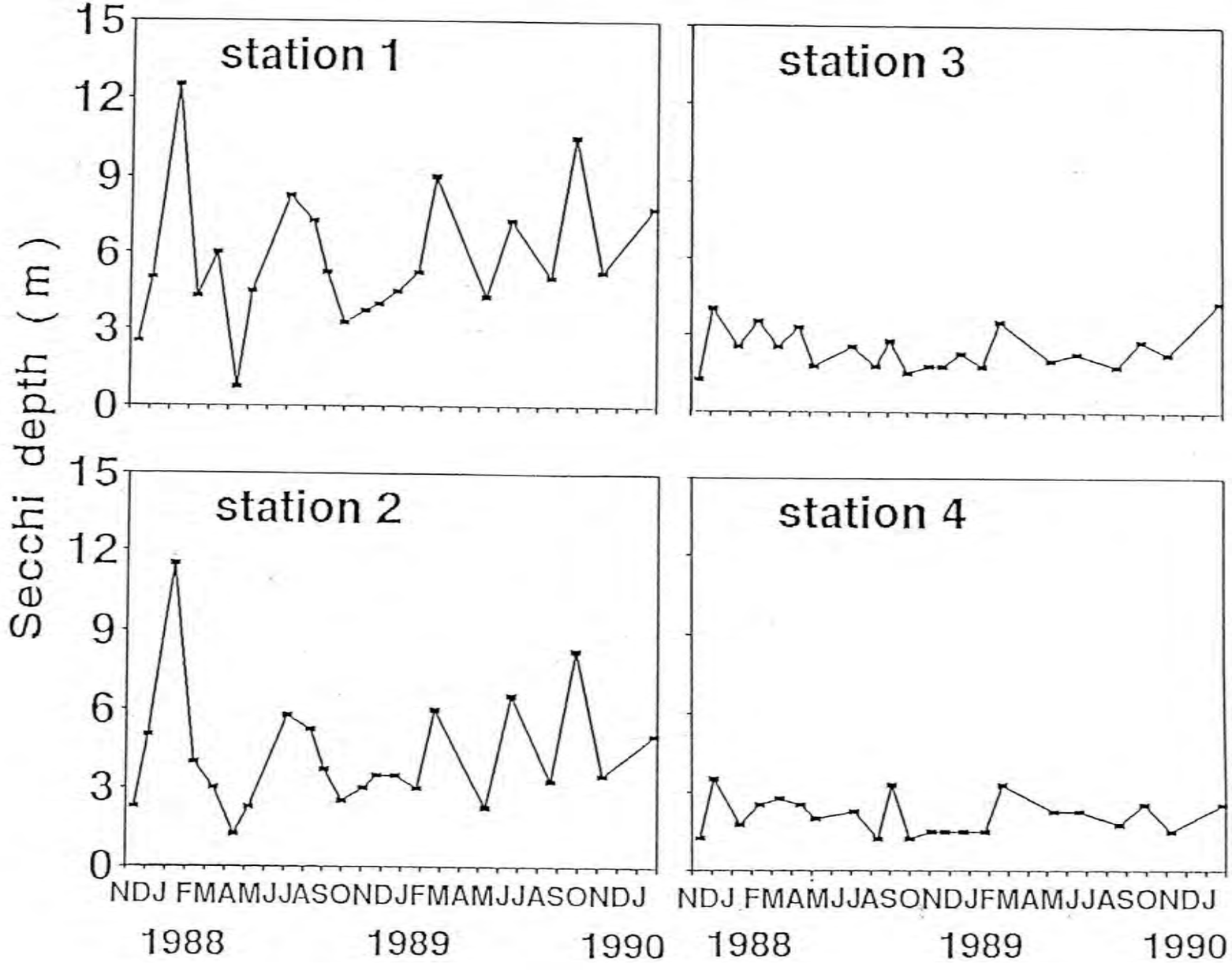

station 1
station 3
station 2
station 4
Secchi depth (m)
0
3
6
9
12
15
NDJ FMAMJJASONDJFMAMJJASONDJ
1988
1989
1990

Fig. 3.6 Concentrations of dissolved inorganic phosphate (▨) and inorganic nitrogen (■) at 4 stations in Tolo Harbour. Each bar represents the mean of measurements taken on January and June 1990.

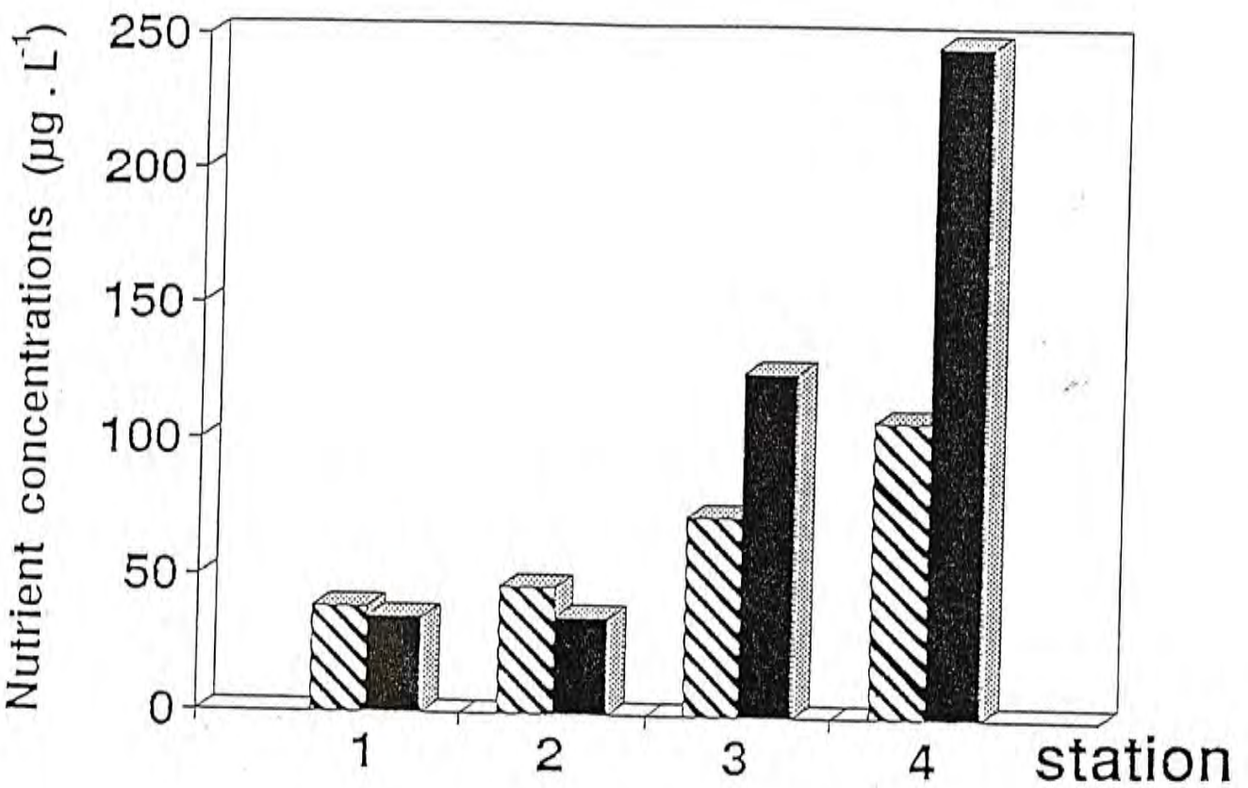
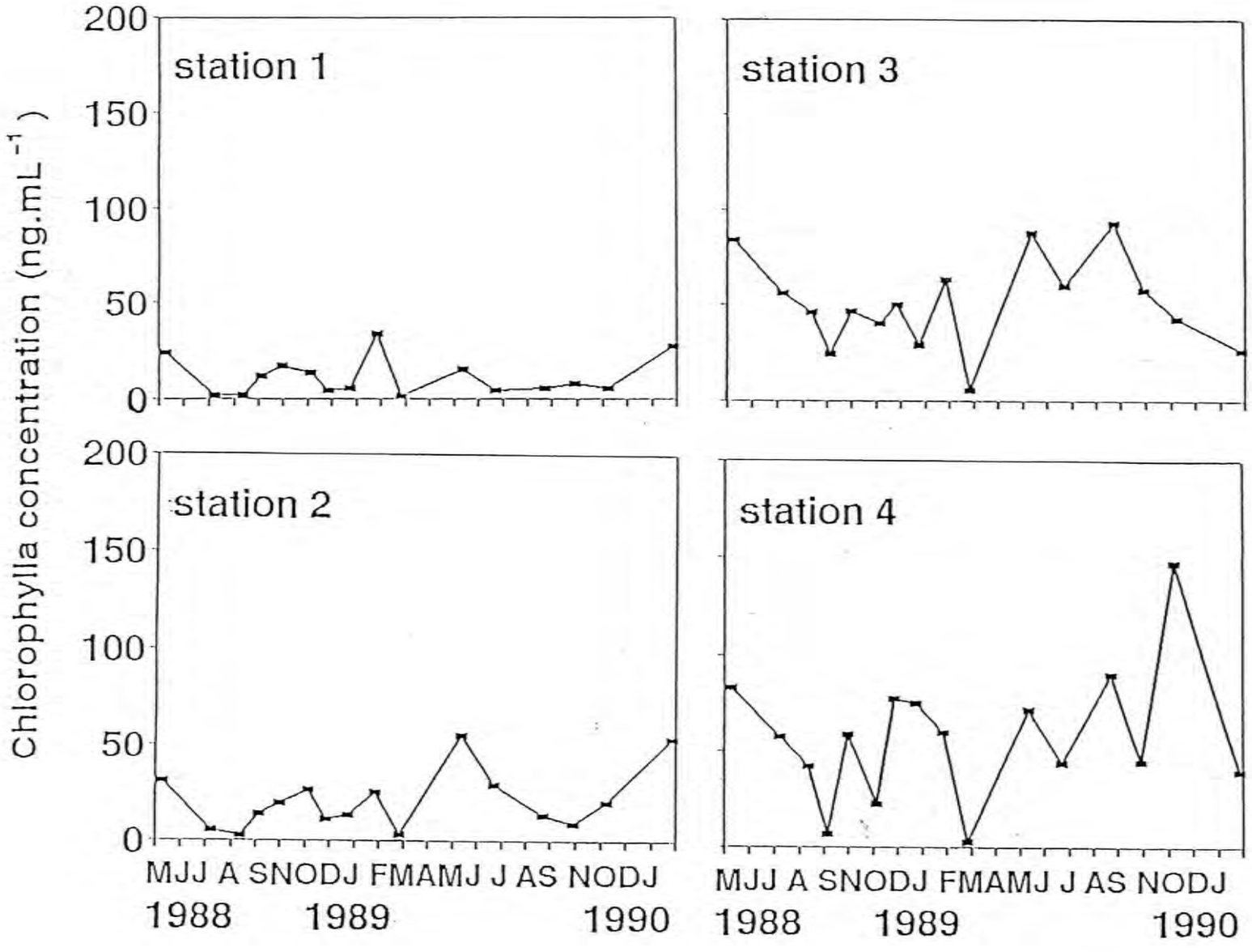

Nutrient concentrations (µg . L-1)
250
200
150
100
50
0
1
2
3
4
station

Fig. 3.7 Concentrations of chlorophyll*a* in surface water collected from 4 stations in Tolo Harbour.


Chlorophylla concentration (ng.mL^{-1})
200
150
100
50
0
station 1
station 3
station 2
station 4
MJJ A SNODJ FMAMJ J AS NODJ
1988
1989
1990

and 50.3 ng.mL^{-1} respectively. In fact, values above 50 ng.mL^{-1} were frequently observed at both stations. Chlorophyll*a* levels at stations 1 and 2 were somewhat lower, but still high compared to unpolluted oceanic waters. Mean concentrations over the study period were 11.3 ng.mL^{-1} at station 1 and 17.9 ng.mL^{-1} at station 2. Marked temporal variation was observed at all stations, although no clear seasonal trends could be detected. Chlorophyll*a* value was closely related to dissolved oxygen concentration and Secchi depth. It showed a positive relationship with dissolved oxygen concentration (Fig. 3.8), and a negative relationship with Secchi depth (Fig. 3.9).

Diatoms and dinoflagellates constituted more than 98% of the total phytoplankton in Tolo Harbour. Spatial variation in the relative contribution of diatoms and dinoflagellates to the total phytoplankton during summer (June, July, August) of 1989 is presented in Fig. 3.10. Average percentage contribution of dinoflagellates to the total phytoplankton was 41.2% at stations 3 and 4 and 64.2% at stations 1 and 2. On the other hand, average percentage contribution of diatoms to the total phytoplankton was 57.0% for stations 3 and 4 and 34.8% for stations 1 and 2.

Marked spatial and seasonal variations in zooplankton dry weight were recorded (Fig. 3.11). With the exception of a single peak of 0.36 g.m^{-3} at station 1 in December 1988, zooplankton dry weights at stations 1 and 2 were generally lower than 0.1 g.m^{-3}. Values in the inner harbour were somewhat higher, with a number of peaks above 0.1 g.m^{-3}. Mean values at

Fig. 3.8 Relationship between chlorophyll*a* and dissolved oxygen in the surface water of Tolo Harbour.

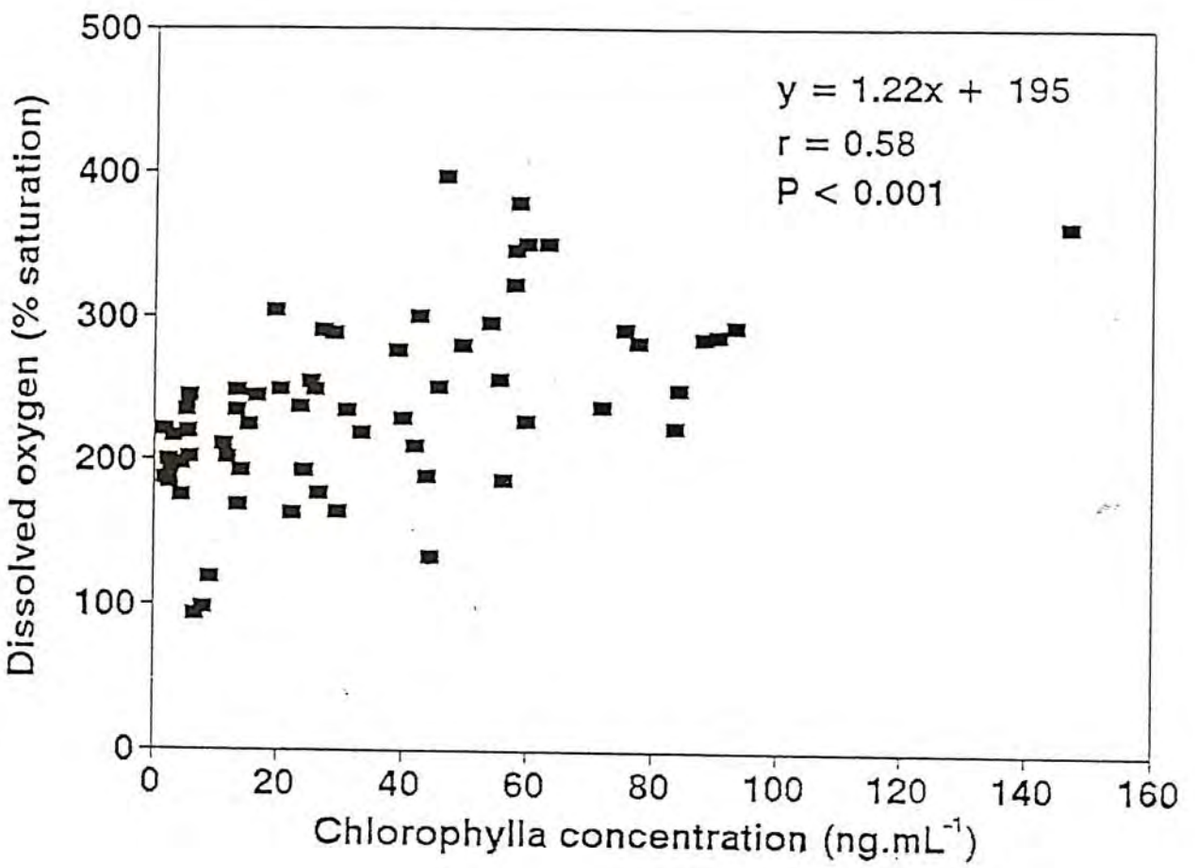

y = 1.22x + 195
r = 0.58
P < 0.001
Dissolved oxygen (% saturation)
Chlorophylla concentration (ng.mL-1)
0
100
200
300
400
500
0
20
40
60
80
100
120
140
160

Fig. 3.9 Relationship between chlorophyll*a* in the surface water and Secchi depth.

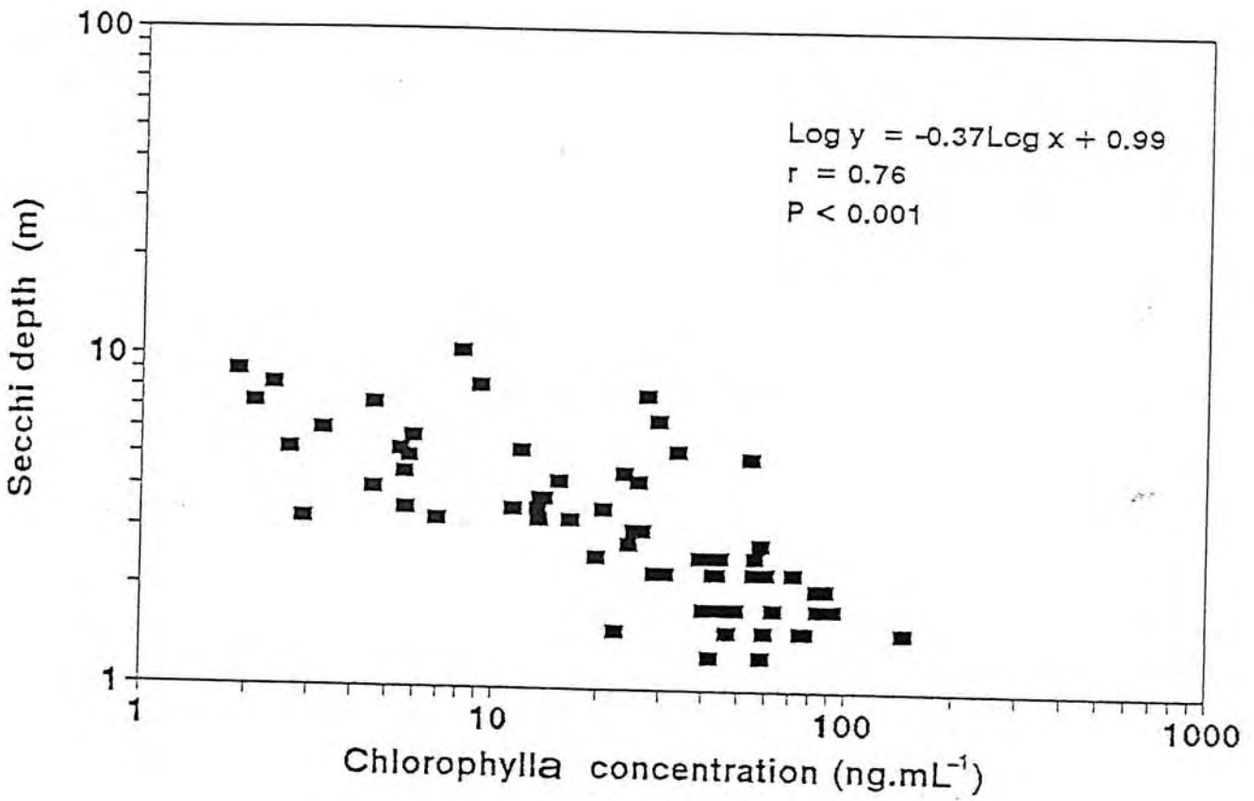
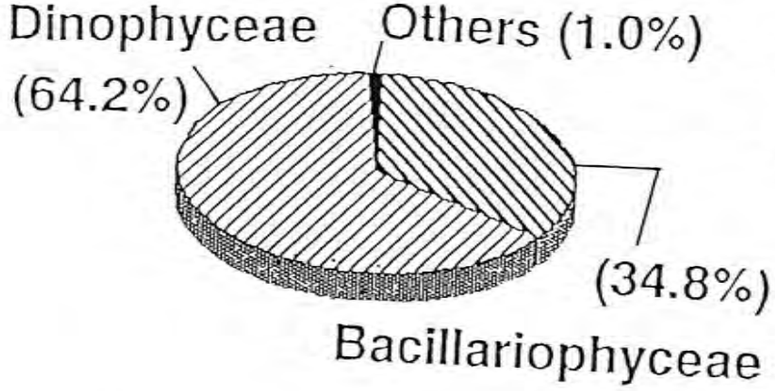

Log y = -0.37Log x + 0.99
r = 0.76
P < 0.001
Secchi depth (m)
100
10
1
1
10
100
1000
Chlorophylla concentration (ng.mL⁻¹)

Fig. 3.10 Percentage contribution of diatoms (Bacillariophyceae) and dinoflagellates (Dinophyceae) to the phytoplankton in Tolo Harbour during summer (June, July, August) of 1989.

stations 1 and 2



stations 3 and 4

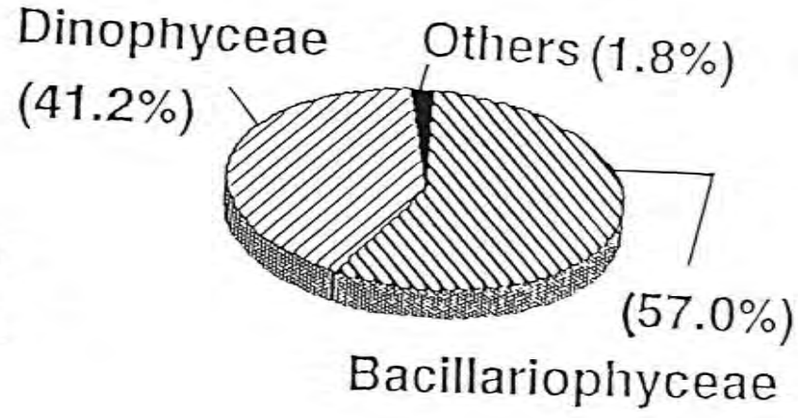
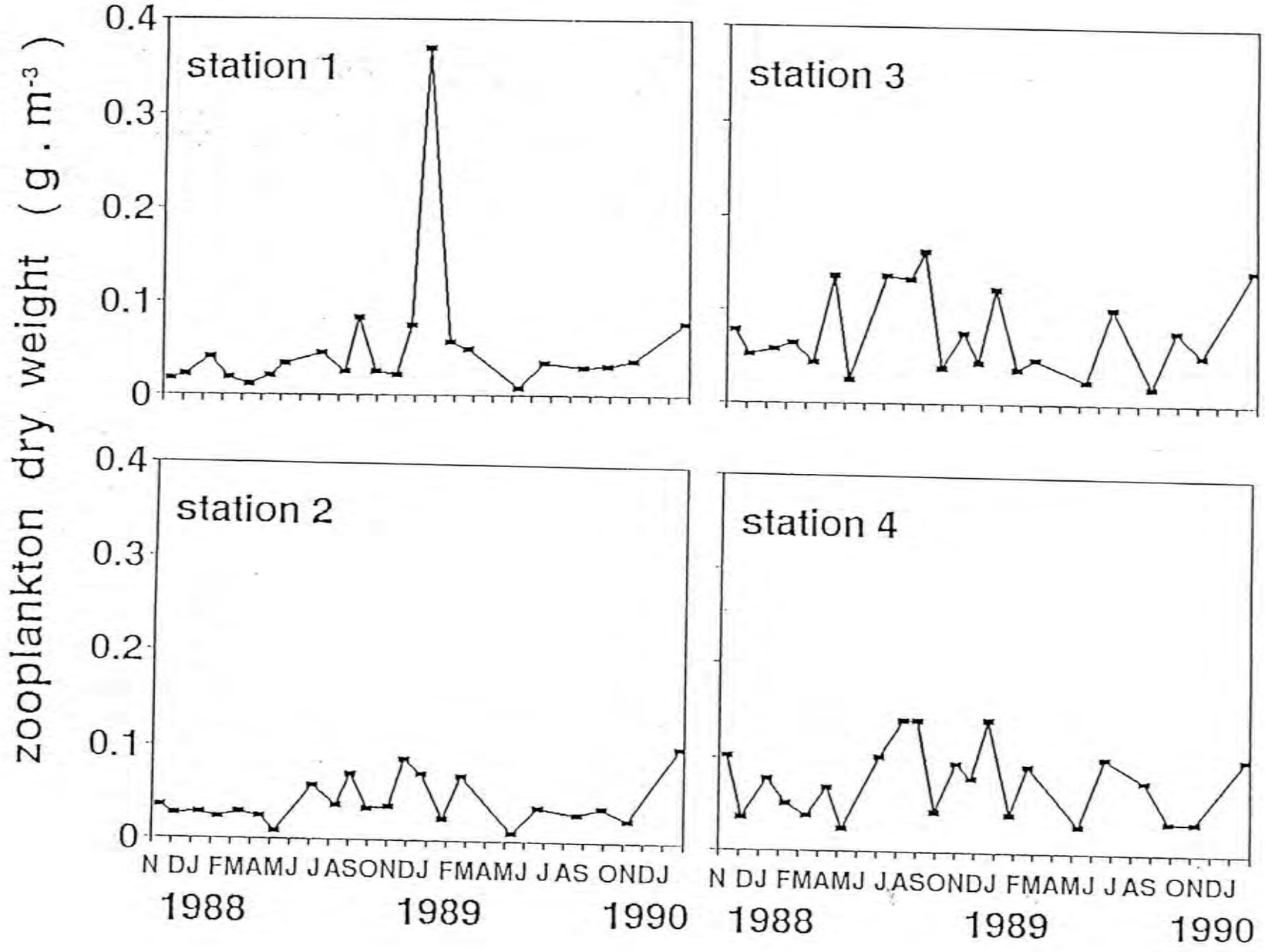


Fig. 3.11 Zooplankton dry weights at 4 stations in Tolo Harbour.


zooplankton dry weight (g.m-3)
station 1
station 3
station 2
station 4
0.4
0.3
0.2
0.1
0
N DJ FMAMJ JASONDJ FMAMJ JAS ONDJ
1988
1989
1990

stations 1, 2, 3 and 4 were 0.05, 0.04, 0.08 and 0.08 $g.m^{-3}$ respectively.

The most important zooplankters in Tolo Harbour and Tolo Channel numerically were crustaceans, principally copepods and cladocerans. Cyclopoid copepods constituted the largest proportion of the crustacean zooplankton in terms of number. The most dominant genera were *Oithona* and *Corycaeus*. Calanoid copepods were the most important component of the zooplankton in terms of species number (Chen 1982). Dominant forms included *Paracalanus*, *Acartia* and *Temora*. Three species of cladocerans, *Penilia avirostris*, *Evadne tergestina* and *Podon* sp., were found. The occurrence of *Podon* sp. was not reported by Chen (1982). In the present study, this species was observed on several occasions in very low number (1 - 2 individuals per net tow).

Population densities of crustacean zooplankton at various stations provided further evidence of landward increase of zooplankton abundance from station 1 to station 4 (Fig. 3.12). Much of the increase could be accounted for by the increase in abundance of Cyclopoida which accounted for 66.7% of the crustacean zooplankton in the inner harbour (Fig. 3.13). Time series of population densities showed several seasonal outbursts of cyclopoid copepods in stations 3 and 4 (Fig. 3.12). Calanoida constituted a smaller proportion of the crustacean zooplankton (Fig. 3.13), but their importance increased towards the mouth of Tolo Channel and their population cycle appeared to coincide with that of cyclopoid copepods in

Fig. 3.12 Seasonal abundance of Cyclopoida (----), Calanoida (——) and Cladocera (—) at 4 stations in Tolo Harbour.

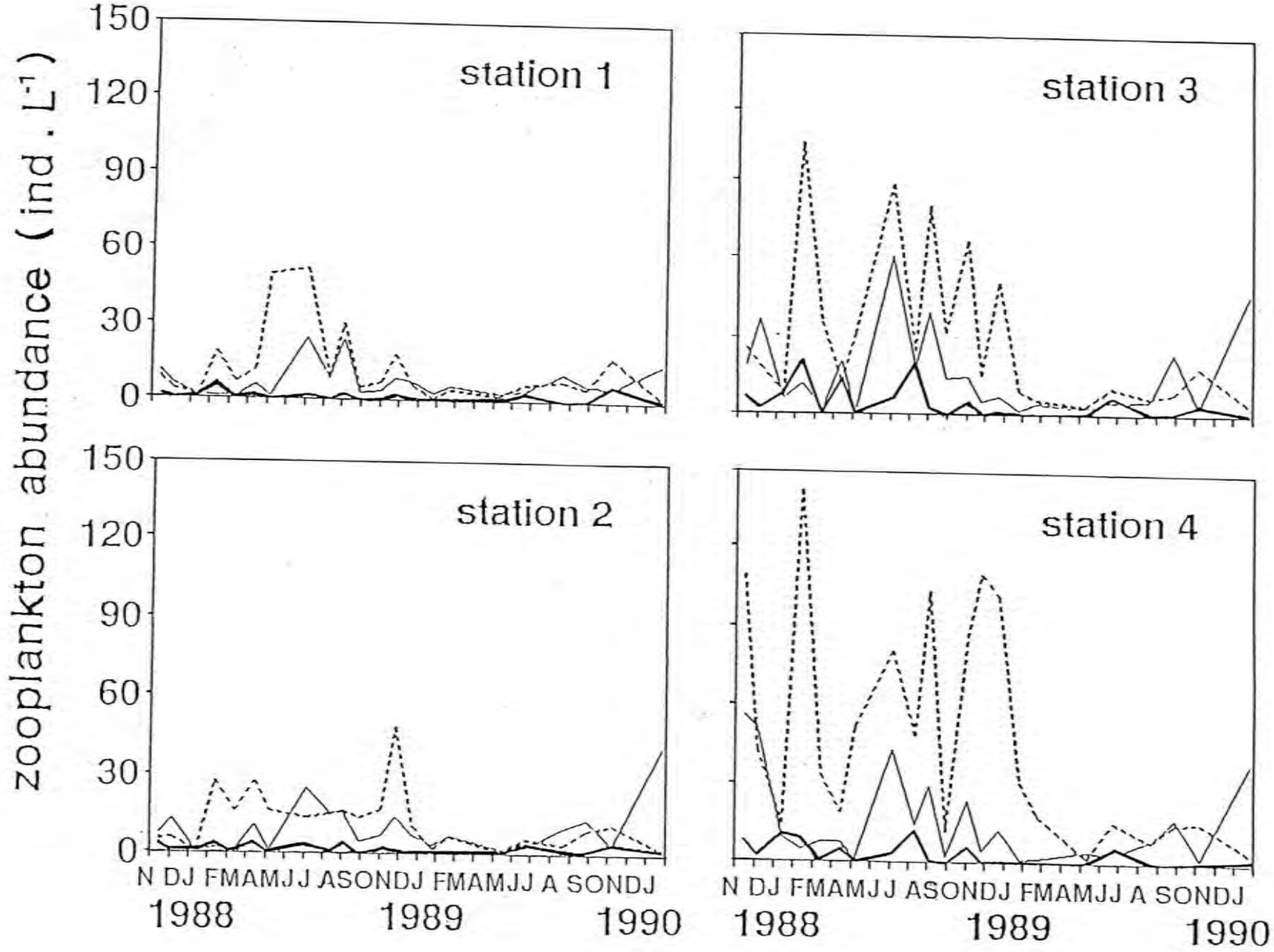
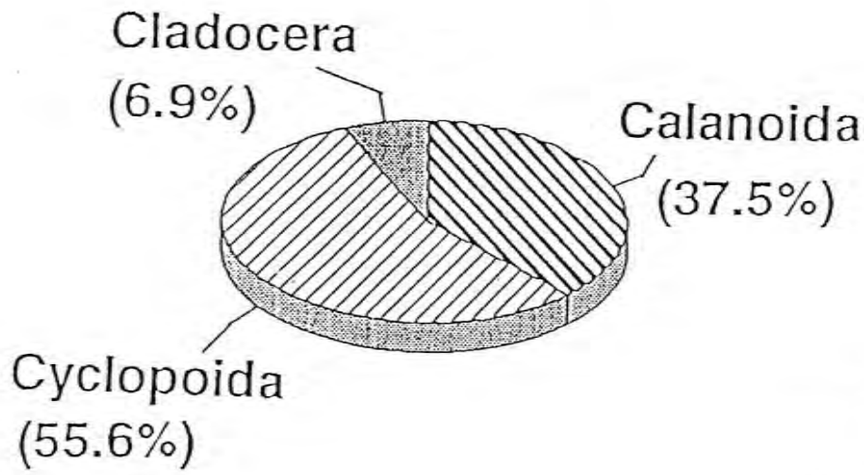
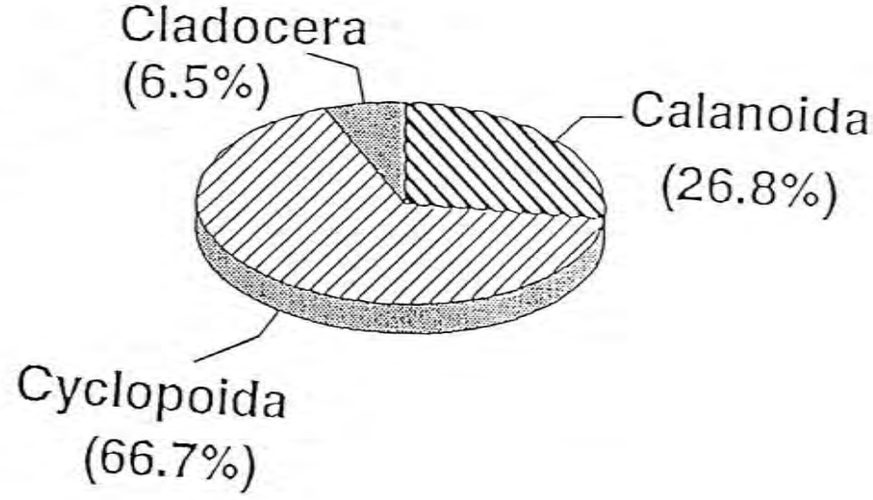

zooplankton abundance (ind . L-1)
150
120
90
60
30
0
station 1
station 3
station 2
station 4
N DJ FMAMJJ ASONDJ FMAMJJ A SONDJ
1988
1989
1990

Fig. 3.13 Percentage contribution of Copepoda, Calanoida and Cladocera to the crustacean zooplankton in Tolo Harbour. Values represent average of 21 sampling dates.

stations 1 and 2



stations 3 and 4



stations 3 and 4. Cladocerans constituted about 7% of the zooplankton in Tolo Harbour. Population densities in the inner harbour were slightly higher than at the channel.

No clear seasonal patterns in zooplankton population could be discerned (Fig. 3.12). Population cycles of cyclopoid and calanoid copepods tended to coincide, especially in stations 3 and 4. Population pattern of cladocerans did not appear to follow those of copepods. Zooplankton abundance appeared to decrease at all stations in 1989. No major population outbursts in marine copepods were recorded in the inner harbour after January 1989. An increase in the abundance of calanoid copepods was observed at all stations during our last sampling in January 1990, but the population densities of Calanoida and Cladocera remained at very low levels.

3.4. Discussion

In Tolo Harbour difference in surface and bottom seawater temperature during summer frequently exceeds 5^{o}C. When the thermally induced density stratification is strengthened by a vertical gradient in salinity (Wear *et al.* 1984), mixing of the entire water column is largely prevented and difference in dissolved oxygen level between surface and bottom waters becomes particularly pronounced. In September and early October, declining air temperature cools the surface water. The results are loss of thermocline and disappearance of density stratification. Eventually, wind-induced circulation produces a fairly homogeneous water mass in terms of dissolved oxygen.

Wear *et al.* (1984) reported that dissolved oxygen level in the surface waters of Tolo Harbour was generally about 100% saturation between 1974 and 1976. Extremely high levels of dissolved oxygen (> 200% saturation) measured in the surface waters during the course of this study indicate a continuing trend of gradual increase in dissolved oxygen level in Tolo Harbour. Good correlation ($r = 0.58$, $P < 0.001$, $n = 64$) between chlorophyll*a* concentration and dissolved oxygen level suggests that supersaturation of oxygen in the surface waters is related to active photosynthesis of the large algal biomass.

The lowest dissolved oxygen value reported by Wear *et al.* (1984)

for the bottom waters of Tolo Harbour was 24.7% saturation. This was recorded in September 1975. Since then, oxygen depletion in the bottom waters of Tolo Harbour has become more severe. Extremely low levels of less than 10% saturation were measured at all stations in June 1988, and the situation is believed to be largely caused by the decomposition of organic matter. Large differences (>5 mg.L^{-1}) in the amount of oxygen present in bottom waters at the beginning and at the end of stratification indicate very high rates of oxygen utilization in the bottom, and therefore reflect a very serious environmental problem.

Concentration of chlorophyll*a* in seawater provides an indirect estimate of the amount of phytoplankton in the water. Wear *et al.* (1984) reported high chlorophyll*a* concentrations in waters close to the Plover Cove in 1975. A single peak of 13500 ng.mL^{-1} was recorded in August, although concentrations during the rest of the year were always below 10 ng.mL^{-1}. Considerably higher concentrations were measured by Chan and Hodgkiss (1987) several years later. In waters close to the Tai Po Sewage Treatment Plant, mean concentrations of 14.36 ng.mL^{-1} and 17.12 ng.mL^{-1} were recorded in 1983 and 1984 respectively. In the channel where nutrient concentrations were lower, mean chlorophyll*a* concentrations only reached 2.69 ng.mL^{-1} in 1983 and 4.12 ng.mL^{-1} in 1984. These values, however, were still considerably lower than those recorded in the present study.

The Secchi depth is influenced mostly by the absorption characteristics of the water and the amount of dissolved and particulate

matters in the water. The negative relationship between Secchi depth and chlorophyll*a* concentration suggests that the observed decrease in water transparency in Tolo Harbour was the result of intense algal growth.

Organic pollution stands as the most important cause for the dramatic increase in phytoplankton biomass in Tolo Harbour. Studies carried out in the 1970's revealed that concentrations of nutrients had already increased in surface waters of Tolo Harbour (Trott 1973; Kueh 1974; Wear *et al.* 1984). Since that time, input of nutrients into Tolo Harbour has increased substantially (Morton 1982; Lam and Ho 1989). In 1984 Hodgkiss and Chan (1987) found that the levels of inorganic phosphate and inorganic nitrogen in the inner harbour were 118.8 $\mu g.L^{-1}$ and 103.9 $\mu g.L^{-1}$ respectively. Results of the present study show that levels of inorganic phosphate in inner Tolo Harbour have not changed significantly since 1984, but concentrations of inorganic nitrogen have increased to between 126.5 and 247.1 $\mu g.L^{-1}$. Wear *et al.* (1984) argued that because nitrogen was the most important limiting nutrient for phytoplankton, higher nitrogen levels and N/P ratios would promote more active algal growth. Indeed, Wu (1988) found good correlation between nitrogen level and phytoplankton standing crop in Tolo Harbour. In addition, significant increase in dissolved nitrogen concentration also explains the alarming increase in phytoplankton biomass. In 1988 and 1989 chlorophyll*a* concentrations in the surface waters reached mean values of about 50 $ng.mL^{-1}$ in the inner harbour and 14 $ng.mL^{-1}$ in the channel. Compared to the earlier studies, these results indicate that eutrophication and intense algal blooms have affected the whole area of Tolo Harbour.

Chlorophyll*a* levels in the water fluctuated considerably throughout the study period, but no obvious seasonal patterns can be discerned. Lam and Ho (1989) suggested that the relatively high winter temperatures in Hong Kong may not suppress algal growth. Correlation between chlorophyll*a* concentration and temperature was poor ($r = 0.1$, $0.20 < P < 0.50$, $n = 64$). A similar lack of seasonal patterns in chlorophyll*a* concentrations was reported by Wear *et al.* (1984).

Shifted species composition and increased dominance of dinoflagellates is evident when our results are compared to those of earlier studies. In 1975 Wear *et al.* (1984) found that the diatom *Chaetoceros* was the dominant phytoplankter in Tolo Harbour. Several years later in 1978 and 1979 Hodgkiss and Chan (1983) reported that diatoms still accounted for 80-90% of the phytoplankton. Since those earlier studies, however, a gradual and steady decline in the dominance of the diatoms was observed. From 1983 to 1984 the percentage contribution of dinoflagellates increased from 11.4% to 25.8% in the inner harbour and from 20.5% to 65.7% in the channel (Hodgkiss and Chan 1987). Increasing dominance of dinoflagellates was accompanied by a progressive decline of the diatoms. Between 1983 and 1984, the percentage contribution of diatoms ranged from 73.4-88.4% in the inner harbour and 32.7-79.0% in the channel. By 1989 the values had declined to 57% in the inner Harbour and 34.8% in the Channel. Associated with increased dominance of the dinoflagellates is a notable increase in the occurrence of red tide and oxygen depletion (Wu 1988; Lam

and Ho 1989).

Evaluation of long term population trends for various groups of crustacean zooplankton is difficult because no regular zooplankton sampling has been conducted in Tolo Harbour. Abundance of crustacean zooplankton showed considerable spatial and temporal variations. Abundance of both phytoplankton and zooplankton were lowest near the mouth of Tolo Channel and increased towards station 4, the inner most station. To some extent, accumulation of phytoplankton and zooplankton in the inner harbour is the result of currents. However, high nutrient supply and slow water movement may also play a role by allowing a zone of high phytoplankton standing crop to develop. Since increased primary production by phytoplankton is expected to eventually give rise to higher zooplankton abundance, it can be speculated that the distribution of herbivorous zooplankton is determined by the availability of their principal food. There was, however, no good correlation between chlorophyll*a* concentration and zooplankton biomass ($r = 0.08$, $P > 0.50$, $n = 64$). While phytoplankton standing crop has increased dramatically during the last several years, comparison with earlier results (Wear *et al.* 1984) indicates only a slight increase in zooplankton dry weight biomass.

An obvious explanation for the poor correlation between chlorophyll*a* concentration and zooplankton biomass is that much of the measured zooplankton dry weight can be accounted by the dinoflagellate *Noctiluca scintillans* which occasionally dominated the plankton community. However, correlation between the number of crustacean zooplankton and

chlorophyll*a* concentration was equally poor ($r = 0.03$, $P >> 0.5$, $n = 64$). As discussed earlier, much of the increase in chlorophyll*a* concentrations in the waters of Tolo Harbour can be attributed to a dramatic rise in the abundance of dinoflagellates. Certain dinoflagellate species are known to produce toxic metabolites (Loeblich and Loeblich 1979; Shimizu 1982). Many herbivorous zooplankton are known to avoid dense patches of toxic dinoflagellates (Fiedler 1982) and reject cells of certain dinoflagellates as food (Huntley *et al.* 1986). In addition, even dinoflagellate species which are not known to be toxic may not be suitable food for herbivorous zooplankton. For instance, Kim *et al.* (1988) observed that while some marine cladocerans occur in dinoflagellates blooms, their feeding is largely restricted to diatoms. Similarly, Huntley *et al.* (1987) found that some dinoflagellates do not contain nutritional factors essential for survival and development of marine copepods.

In Tolo Harbour increase dominance of toxic or inedible dinoflagellates may have already adversely affected the crustacean zooplankton. The population densities of both copepods and cladocerans decreased markedly during 1989. To date, it is not known whether the decrease was part of natural population fluctuation or the beginning of a long term decline triggered by deteriorating water quality and competitive dominance of dinoflagellates. However, since oxygen depletion in the bottom waters was not particularly severe in 1989, it is probable that the competitive dominance of dinoflagellates is at least partly responsible.

Significant correlation occur between zooplankton density and temperature ($r = 0.23$, $P < 0.05$, $n = 64$), but no clear seasonal patterns in zooplankton abundance can be identified. While the zooplankton community in Tolo Harbour is diverse, seasonal succession of individual species is not apparent. The occurrence of large populations of zooplankton in the winter is mostly due to warm temperature and high levels of primary production (Chan and Hodgkiss 1987). For example, marine cladocerans, which have been observed to occur most frequently during the warmer seasons in the northwestern Pacific (Yoo and Kim 1987), displayed no clear seasonal patterns in the subtropical waters of Tolo Harbour.

This study represents the latest in a series of attempts to document the biological impacts of organic pollution in Tolo Harbour. The results confirm that water quality has continued to deteriorate and eutrophication has impacted the marine plankton. While the small size and transient nature of plankton patches may account for the lack of distinctive seasonal trends, long term changes including increases in phytoplankton standing crop, decreases in zooplankton abundance and changes in species composition are clearly identifiable.

Chapter 4

Seasonal dynamics of crustacean zooplankton in Tolo Harbour

4.1. Introduction

Because of the clear relationship between nutrient loading and primary production, the phytoplankton in Tolo Harbour has been studied extensively by several authors (e.g. Chan and Hodgkiss 1987; Hodgkiss and Chan 1987; Lam and Ho 1989). In general, their findings confirmed that increased nutrient levels have led to increases in phytoplankton biomass, changes in phytoplankton species component and markedly increased in number of red tide blooms. While zooplankton forms a major trophic link between primary production and fish, very little is known about its ecology and biological importance in Tolo Harbour. According to a recent systematic survey by Chen (1982), copepods and cladocerans formed the most important component of the marine zooplankton in the coastal waters of Hong Kong in terms of both abundance and species diversity. Wear *et al.* (1984) gave an account of the zooplankton dry weight in Tolo Harbour, but presented no data on species composition and population dynamics. This chapter presents the result of a study carried out between November 1987 and January 1990 to investigate the seasonal dynamics of crustacean zooplankton in Tolo Harbour. In view of the rapid deterioration of Tolo Harbour as a habitat for aquatic organisms, such an investigation is clearly of interest to marine biologists.

4.2. Materials and Methods

Zooplankton was collected from 4 sampling stations in Tolo Harbour at roughly monthly intervals between November 1987 and January 1990. Location of the sampling stations was chosen to represent both the shallow and low-salinity waters of the inner harbour and the deeper and more oceanic waters of the channel (Fig. 3.1). Detailed description of sampling and collecting procedures was presented in Chapter 3. Zooplankton from each net haul was preserved in 4% formaldehyde and concentrated in 100 mL plastic bottles. Zooplankton abundance was estimated by counting at least 6% of each sample under a stereomicroscope. Zooplankton was identified to genera according to the taxonomic guide of Cheng *et al.* (1988)

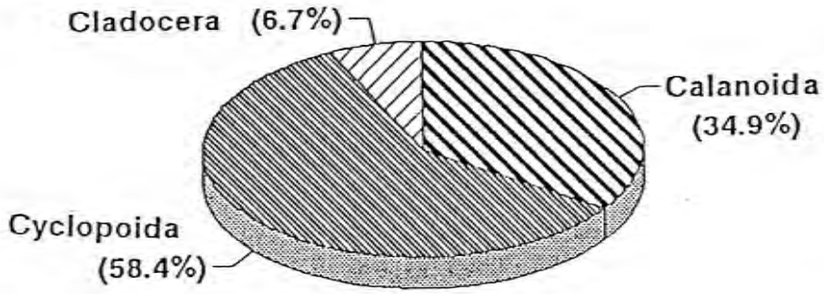
4.3. Results

The percentage composition of Cyclopoida, Calanoida and Cladocera to the total zooplankton population in Tolo Harbour is presented in Fig. 4.1. With percentage contribution at the various sampling stations ranging from 53% to 72%, cyclopoid copepods strongly dominated the zooplankton community. Calanoid copepods were the second most abundant zooplankter in Tolo Harbour. Their percentage contribution increased from 23.3-31.3% in the inner harbour to 34.9-40.0% in the channel. Cladocerans (*Penilia* and *Evadne*) were found at all sampling stations, but their percentage contribution to the marine zooplankton was never more than 10%.

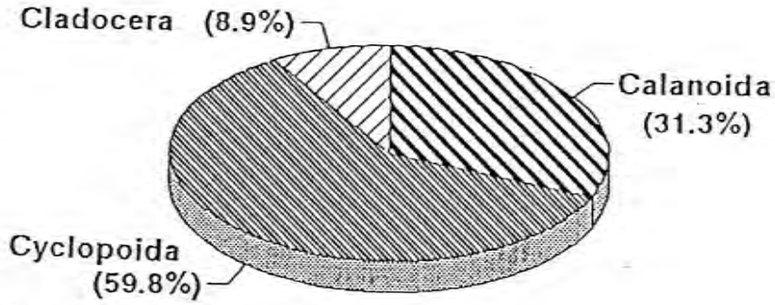
Fig. 4.2 illustrates the density of Cyclopoida, Calanoida and Cladocera at 4 sampling stations. Highest densities were observed at station 4, the inner most station. Densities of Cyclopoida and Calanoida were lowest at station 1 and increased progressively towards station 4 (Fig. 4.2). Similarly, density of Cladocera was highest at station 3, outside the highly eutrophic fish culture zone in Tai Po Hoi, and lowest at station 1, near the outlet of Tolo Harbour. Clear dominance of Cyclopoida in the zooplankton community was observed at all sampling stations. Average density of Cyclopoida at station 4 was more than 45 ind.L^{-1}.

Fig. 4.1 Percentage contribution (average of 21 sampling dates) of Cyclopoida, Calanoida and Cladocera to the total crustacean zooplankton at 4 stations.

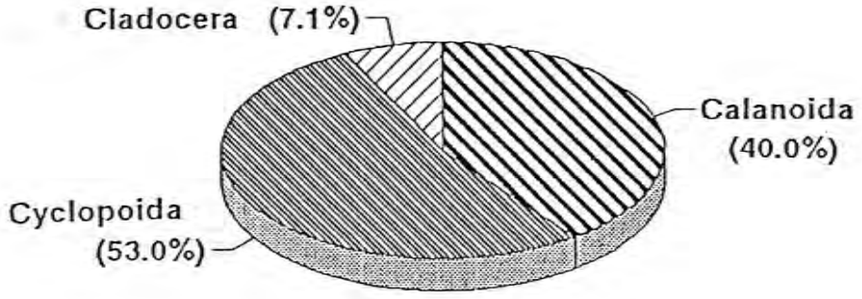
station 1



station 3



station 2



station 4

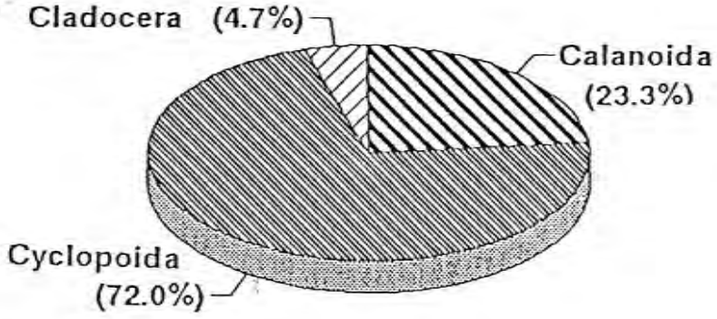


Fig. 4.2 Density of Cyclopoida (▨), Calanoida (■) and Cladocera (⊠) at 4 stations. Each bar represents the average of 21 sampling dates.

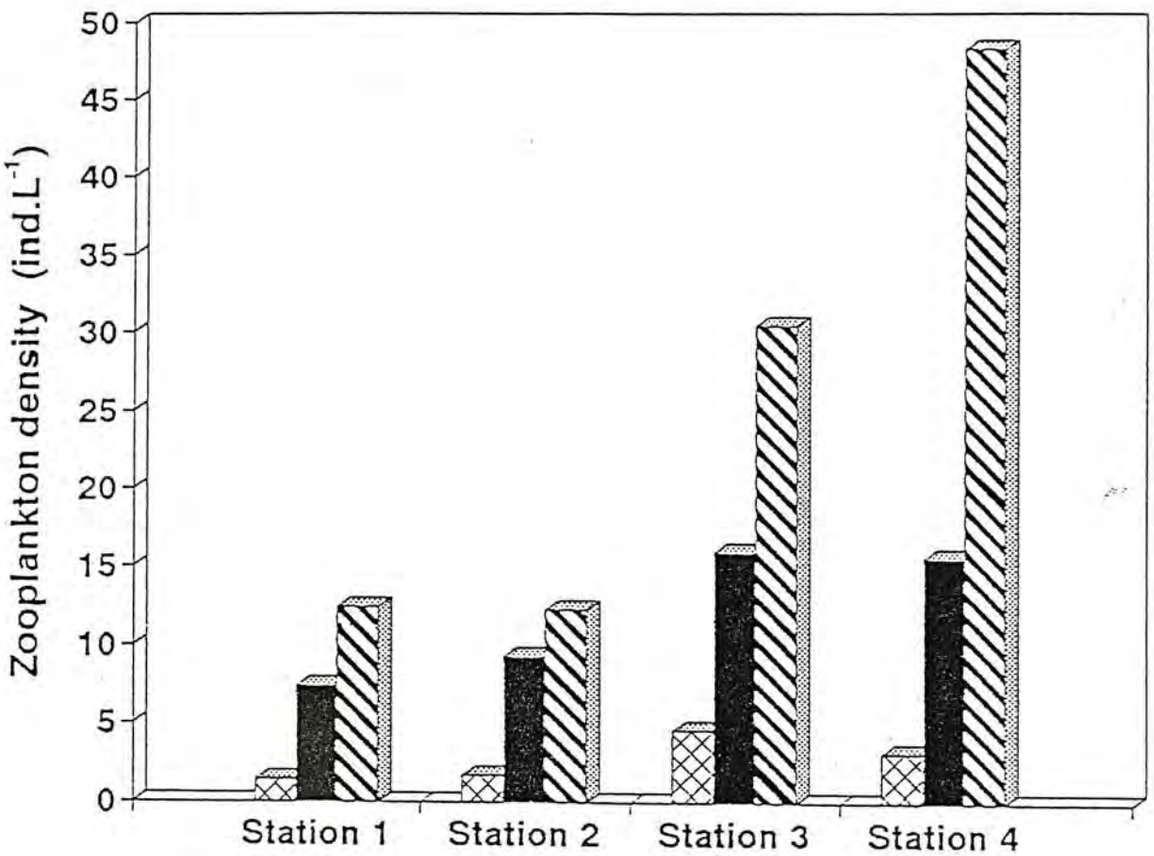

Zooplankton density (ind.L-1)
50
45
40
35
30
25
20
15
10
5
0
Station 1
Station 2
Station 3
Station 4

Fig. 4.3 illustrates the percentage contribution of several major copepod genera to the copepod community in Tolo Harbour. *Oithona* was the most dominant. *Paracalanus* ranked second. Strong domination of the zooplankton community by *Oithona* was observed at all 4 stations, and was particularly complete at station 4 where *Oithona* comprised 66.3 % of the copepod community. Other common copepod genera included *Corycaeus*, *Acartia* and *Temora*.

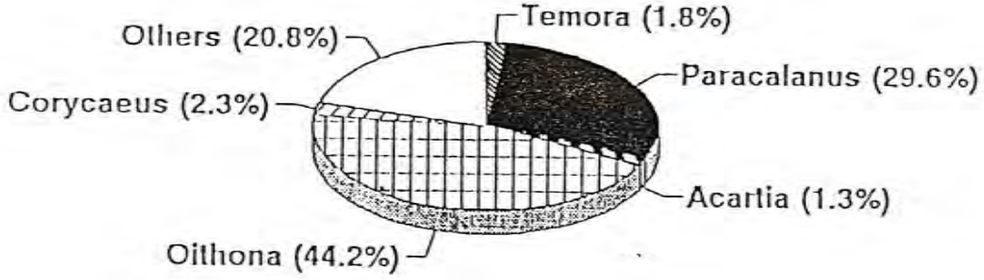
Two genera of cladocerans, *Penilia* and *Evadne*, were commonly found in Tolo Harbour (Fig. 4.4). *Penilia* was slightly more common than *Evadne* at station 1, but the importance of *Evadne* appeared to increase landward. At station 3 *Evadne* comprised 61.5% of all cladocerans.

Temporal variations in the abundance of *Oithona* and *Corycaeus* at 4 sampling stations are presented in Fig. 4.5. Marked temporal variations were observed, although no clear seasonal patterns could be found. Densities of *Oithona* and *Corycaeus* were highest in January and February 1988 and declined slowly but consistently during the rest of the study period. Highest densities for both genera were found at station 4 and lowest densities were found at station 1.

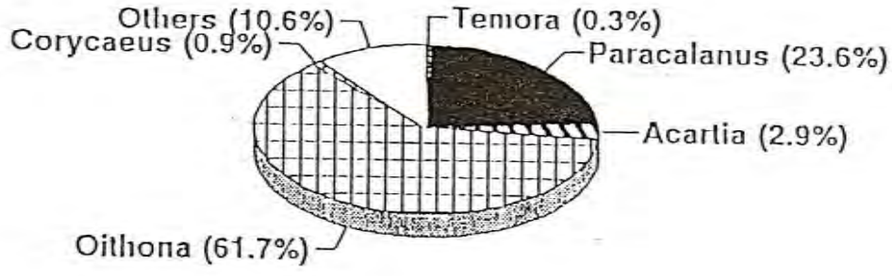
Tolo Harbour supported a very high diversity of calanoid copepods.

Fig. 4.3 Percentage contribution (average of 21 sampling dates) of *Temora, Paracalanus, Acartia, Oithona* and *Corycaeus* to the Copepoda community at 4 stations.

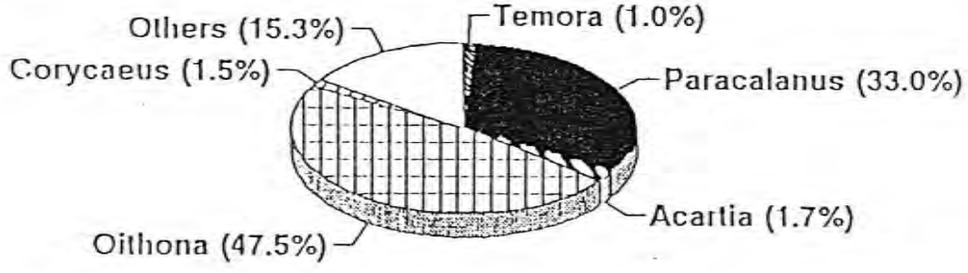
Station 1



Station 3



Station 2



Station 4

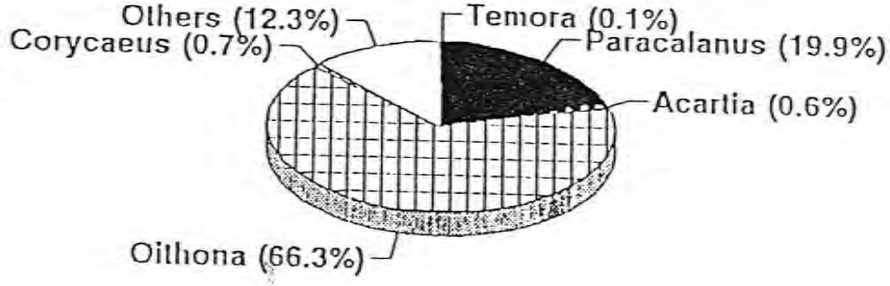
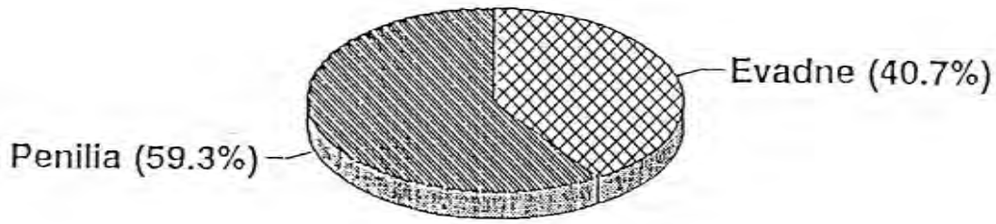
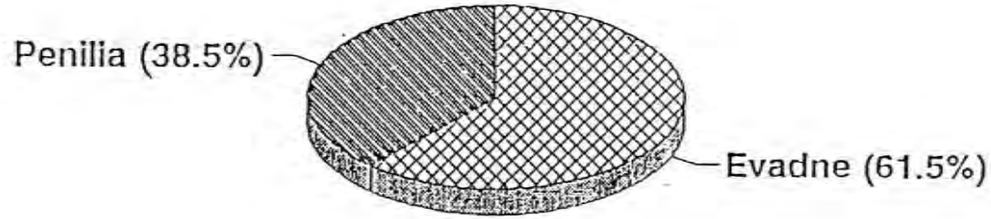


Fig. 4.4 Percentage contribution (average of 21 sampling dates) of *Penilia* and *Evadne* to the Cladocera community at 4 stations.

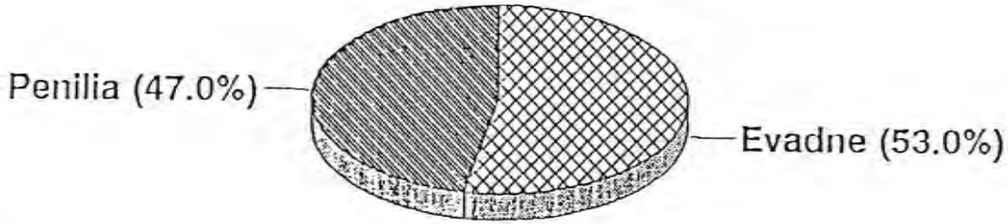
station 1



station 3



station 2



station 4

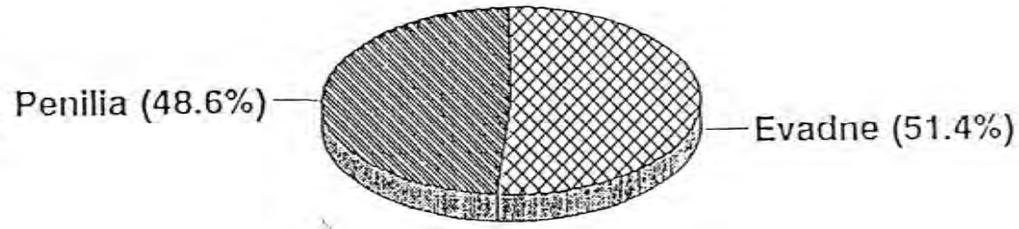
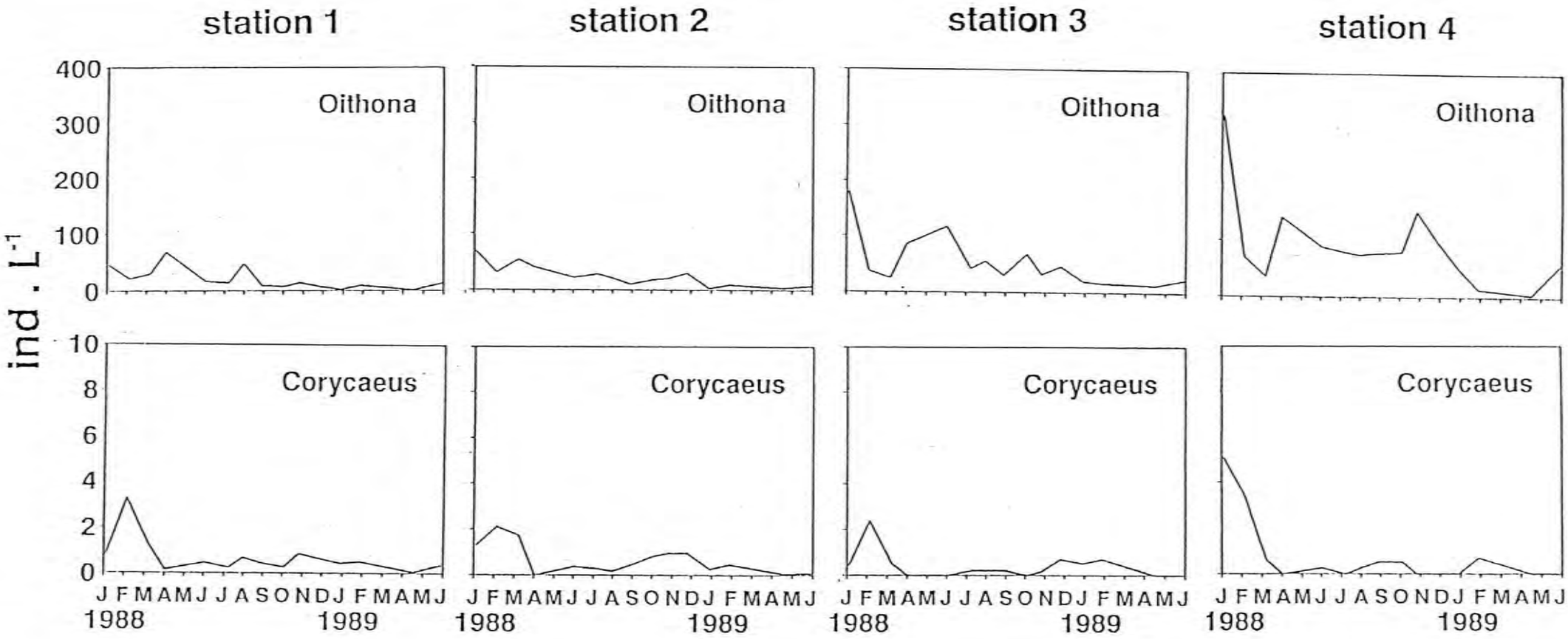


Fig. 4.5 Seasonal abundance of *Oithona* and *Coryceaus* at 4 stations.


station 1
station 2
station 3
station 4
Oithona
Corycaeus
ind . L-1
400
300
200
100
0
10
8
6
4
2
0
J F M A M J J A S O N D J F M A M J
1988
1989

The seasonal abundance of the 3 most abundant genera at 4 sampling stations is presented in Fig. 4.6. Again, the results show marked temporal variations with no clear seasonal patterns. *Paracalanus* was the most abundant, followed by *Acartia* and *Temora*. All 3 genera occurred in large populations between May and November. Generally, the populations started to increase around April, then decreased to much lower levels in August and September. For *Temora* numbers started to increase again in September and peaked in late October and early November. A similar pattern was found for *Acartia* in the inner harbour. All 3 genera occurred in very low numbers during the winter.

In addition to temporal variations, *Paracalanus*, *Acartia* and *Temora* showed significant differences in their spatial distribution (Fig. 4.6). Abundance of *Paracalanus* and *Acartia* was highest in the inner Harbour and declined slightly towards Tolo Channel. In contrast, *Temora* occurred at higher densities in Tolo Channel than in the inner harbour.

Fig. 4.7 illustrates the seasonal dynamics of cladocerans *Penilia* and *Evadne* at 4 sampling stations in Tolo Harbour. Spatial and temporal variations in the number of *Penilia* and *Evadne* were high. *Evadne* exhibited 3 marked peaks in February, April and August of 1988. Although 3 population maxima also occurred for *Penilia*, they did not coincide

Fig. 4.6 Seasonal abundance of *Paracalanus, Acartia* and *Temora* at 4 stations.

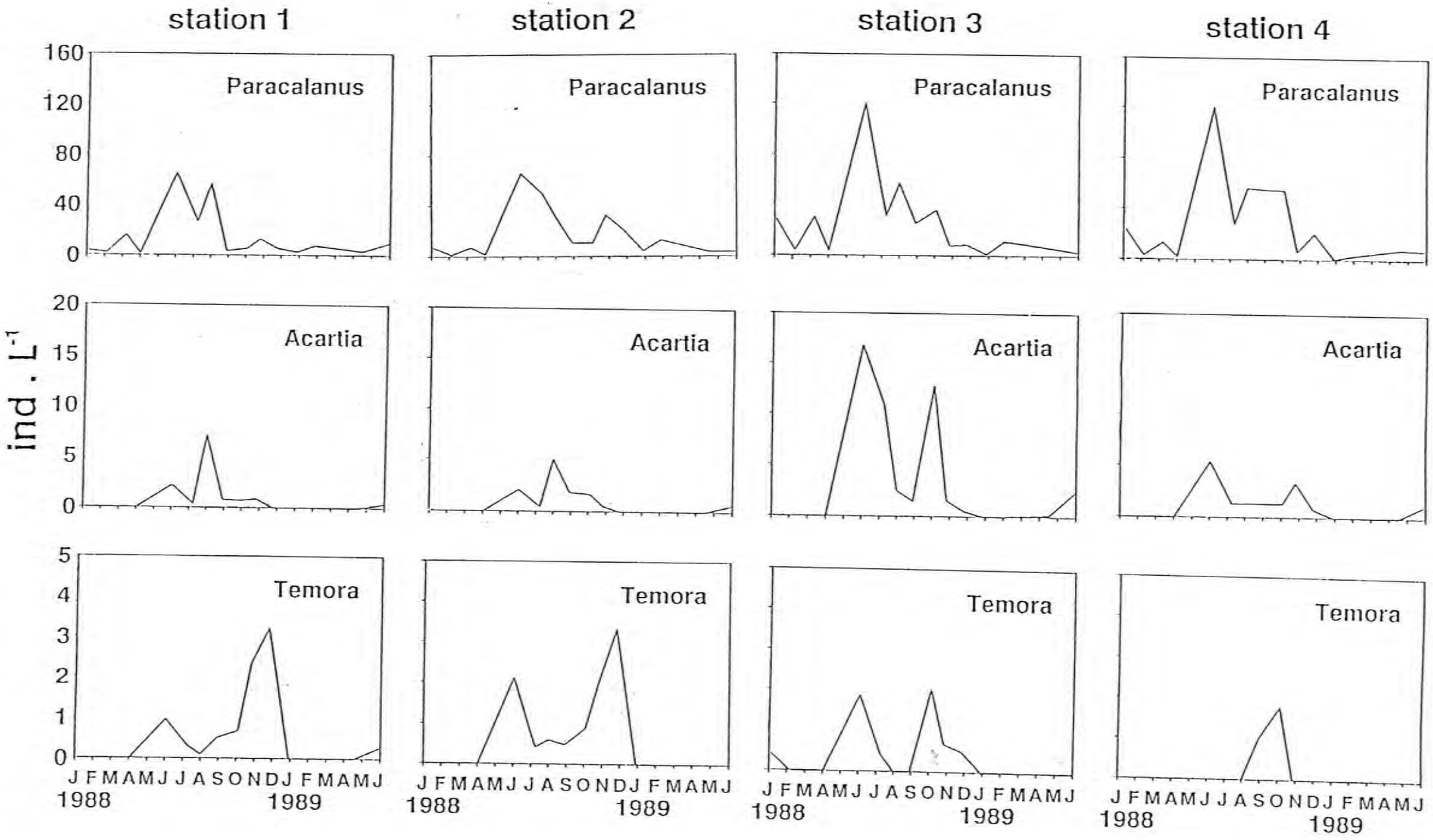
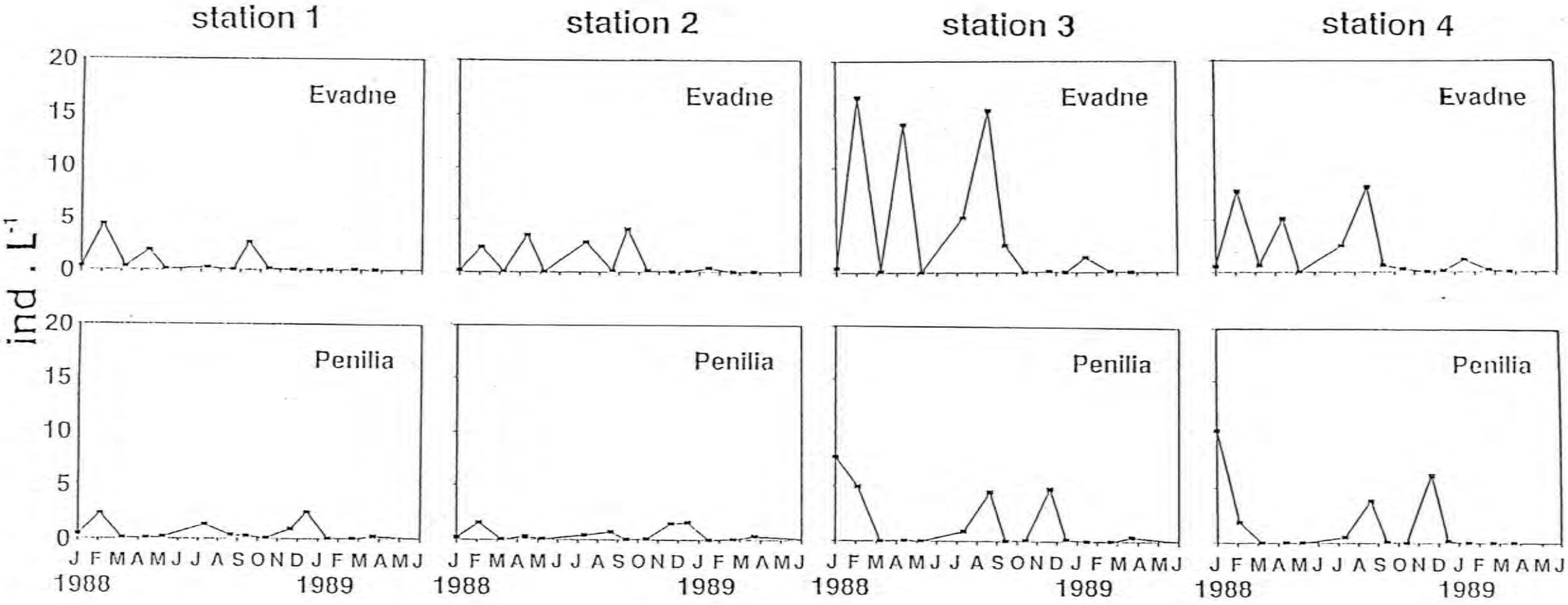

station 1
station 2
station 3
station 4
Paracalanus
Acartia
Temora
ind . L-1
160
120
80
40
0
20
15
10
5
4
3
2
1
J F M A M J J A S O N D J F M A M J
1988
1989

Fig. 4.7 Seasonal abundance of *Evadne* and *Penilia* at 4 stations.


station 1
station 2
station 3
station 4
Evadne
Penilia
ind . L-1
20
15
10
5
0
J F M A M J J A S O N D J F M A M J
1988
1989

temporally with those of *Evadne*. In general, the population dynamics of the cladocerans did not appear to show clear seasonal patterns. The number of *Evadne* and *Penilia* declined drastically after December 1988, and no population maxima were observed in 1989. Both cladocerans showed landward increase in population. Populations at stations 3 and 4 in the inner harbour were generally larger than those at stations 1 and 2 in the channel.

Table 4.1 provides the mean values of hydrographical parameters and zooplankton abundance for 1988 and 1989.

Table 4.1. Summary of physical and biological variables in Tolo Harbour for 1988 and 1989. Each value represents the average of 4 sampling stations.

	1988	1989	P*
Dissolved oxygen (% saturation)			
surface	163.31	166.35	< 0.100
bottom	90.72	112.93	< 0.005
Chlorophyll*a* ($ug.L^{-1}$)	31.45	39.40	< 0.500
Total zooplankton ($ind.L^{-1}$)	52.50	12.82	< 0.001
Cyclopoida ($ind.L^{-1}$)	37.49	8.90	< 0.001
Calanoida ($ind.L^{-1}$)	11.56	5.94	< 0.001
Cladocera ($ind.L^{-1}$)	3.45	1.45	< 0.002

* Probability of no difference between 1988 and 1989 is tested by Student's *t*-test.

4.4. Discussion

Biomass of both phytoplankton and zooplankton increased from the more oceanic waters of the channel (stations 1 & 2) to the shallow estuarine waters of the inner harbour (stations 3 & 4). High nutrient supply and slow water movement allowed phytoplankton to grow rapidly in the inner harbour. In theory, the stable environment with its high food availability, permits herbivorous zooplankton to accumulate in large numbers.

Copepods generally constitute the largest component of the marine zooplankton (see Russell and Colman 1934; Wickstead 1961; Reeve 1964, 1970). Moore (1967) found that the average frequency of copepods in Kingston Harbour was 43% in the upper basin and 34% in the outer harbour. In Tolo Harbour, copepods comprised more than 90% of the crustacean zooplankton. Abundance of Cyclopoida increased significantly from Tolo Channel to the inner regions of Tolo Harbour. Percentage contribution of the Cyclopoida to the total zooplankton was 58.4% in station 1, and increased to 72% in station 4. *Corycaeus* and *Oithona* together made up more than 95% of the cyclopoid copepod community in Tolo Harbour. *Oithona*, in particular, strongly dominated in the zooplankton in all areas of Tolo Harbour. Chen (1982) reported that *Corycaeus* and *Oithona* were common in Hong Kong waters mostly during spring. However, results of this study reveal that *Oithona* appears to dominate the zooplankton in Tolo Harbour throughout the whole year. Dominance of *Oithona* in Tolo

Harbour suggests that the occurrence of this genus may be associated with eutrophic coastal waters.

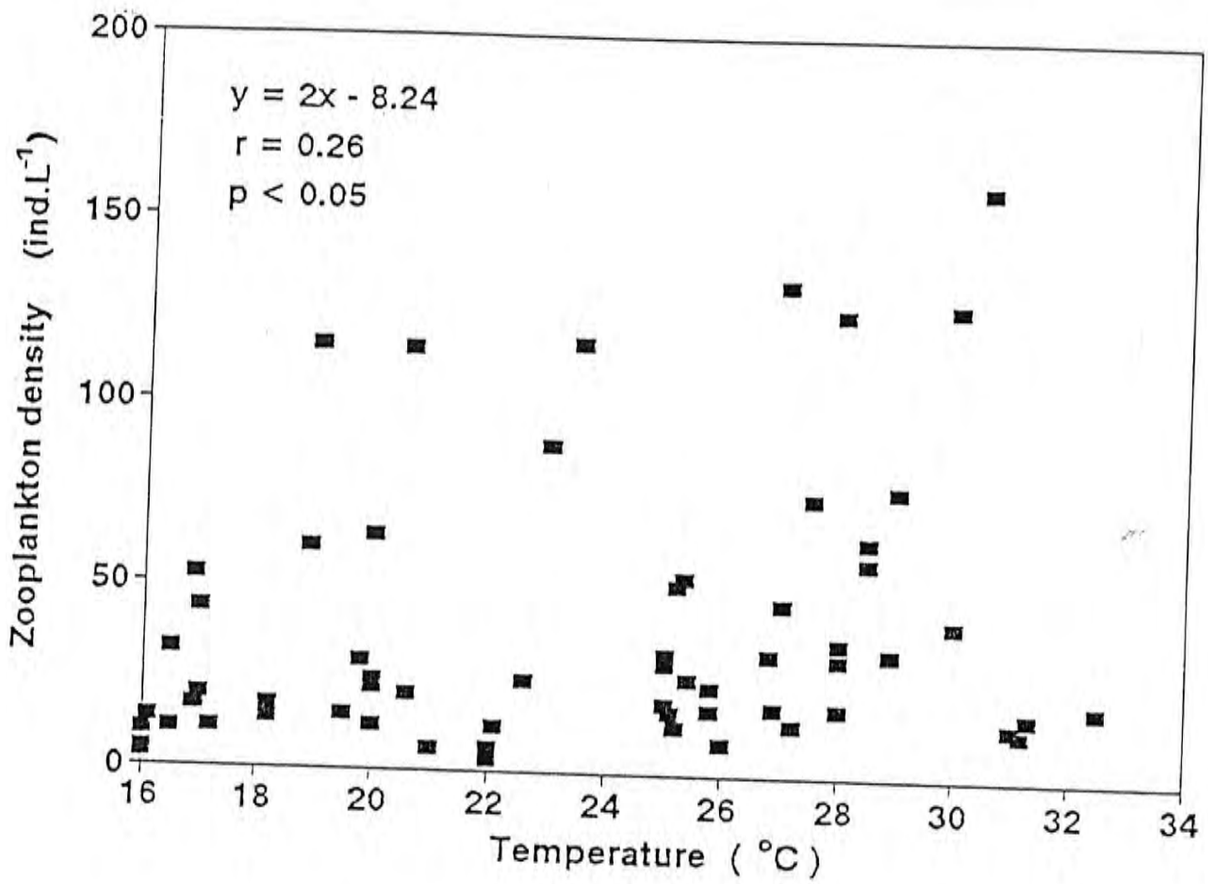
Calanoid copepods formed a large proportion of the total zooplankton population in Tolo Harbour. The 3 most common genera are *Paracalanus*, *Temora* and *Acartia*. *Paracalanus* is known to be of widespread distribution, living and reproducing in the neritic regions of Po-Hai Gulf, the Yellow Sea and the East China Sea (Chen 1982). It was by far the most common calanoid copepod in Tolo Harbour and was particularly numerous in the shallow inner regions of embayment. Chen (1982) reported that the highest number of *Paracalanus* and *Acartia* was found in summer and early autumn, while *Temora* was most abundant in spring and winter. In generally, very similar patterns of occurrence were found for these calanoid copepods in Tolo Harbour. *Paracalanus* and *Acartia* exhibited population maxima early in the summer. Population of *Temora*, on the other hand, reached a peak in May and June, declined to very low levels in the middle of the summer, and then increased to another peak in early winter.

In temperate oceans, marine cladocerans are most commonly found in the zooplankton between spring and autumn (Yoo and Kim 1987). *Evadne nordmanni*, for example, occurs from late spring to autumn in the North Atlantic and North Sea (Gieskes 1971; Platt 1977). In tropical and subtropical waters of the Indian Ocean, the seasonal distribution is different with *E. tergestina* occurring throughout the whole year and *Penilia avirostris* found mainly from September through March (Pillai and Pillai 1975). In the

coastal waters of China, *P. avirostris* and *E. tergestina* show a similar pattern of seasonal occurrence, with the earlier appearance of *P. avirostris* in southern waters near Taiwan Strait, Hong Kong and Hainan Strait (Cheng and Chao 1982). In Tolo Harbour *Penilia* and *Evadne* did not exhibit well defined patterns of seasonal occurrence. Temporal variatons in population size was characterized by irregular fluctuations with a series of peaks in 1988, and a noticeable decrease in numbers in 1989.

Temperature and primary production seem to be the major environmental factors controlling the seasonal distribution of marine zooplankton. Significant correlation ($r = 0.26$, $P < 0.05$, $n = 64$) was found between zooplankton density and temperature in Tolo Harbour (Fig. 4.8). Kiorboe *et al.* (1988) observed that copepod populations in many shallow temperate oceans are controlled by temperature rather than by phytoplankton abundance. Similarly, Onbé (1977) reported that the seasonal occurrence of marine cladocerans in the warm waters of the Inland Sea of Japan is controlled by temperature. These observations are supported by studies showing that the biology of marine zooplankton was greatly affected by temperature. For instance, feeding rates (Deason 1980; Kiorboe *et al.* 1982; Dagg and Wyman 1983), development rates (Corkett and McLaren 1978; McLaren 1978; McLaren and Corkett 1981; Smith and Lane 1985) and egg production rates (Corkett and McLaren 1978; McLaren 1978; Smith and Lane 1985; Kiorboe *et al.* 1988) of marine copepods are substantially increased by warmer temperature. Warmer water

Fig.4.8 Relationship between surface water temperature and zooplankton density.


y = 2x - 8.24
r = 0.26
p < 0.05
Zooplankton density (ind.L-1)
Temperature (°C)
0
50
100
150
200
16
18
20
22
24
26
28
30
32
34

temperatures during winter may lead to elevated reproductive rates in winter and early spring, shorter periods of diapause, or enhanced survival of overwintering populations. Any of these factors may, in turn, result in higher reproductive stocks in early spring and higher overall copepod populations during summer.

Chen (1982) concluded that high primary production provided nourishment for the zooplankton and allowed its number to increase more rapidly. Chan and Hodgkiss (1987) also argued that the occurrence of large populations of zooplankton in Tolo Harbour was primarily due to high levels of primary production. In the present study, no significant correlation was found between chlorophyll*a* concentration and zooplankton abundance ($r = 0.03$, $P >> 0.5$, $n = 64$). As indicated in Chapter 3, a very large proportion of the total phytoplankton in Tolo Harbour consisted of dinoflagellates and many forms of red tide dinoflagellate are toxic to marine zooplankton (Huntley *et al.* 1986). Although none of the dinoflagellate species in Tolo Harbour have been known to associate with the paralytic shellfish poisoning (PSP), neurotoxic shellfish poisoning (NSP) or diarrhetic shellfish poisoning (DSP) (Holmes and Lam, 1985), dinoflagellate blooms may still have non-toxic impacts on the population dynamics of planktonic organisms. For example, dominant dinoflagellates such as *Noctiluca scintillans* are too large to be ingested by crustacean zooplankton. Other smaller forms may not contain nutritional factors essential for survival and reproduction of zooplankton. Kim *et al.* (1988) reported that marine cladocerans feed mainly on diatoms. Thus, increased dominance of dinoflagellates in the total phytoplankton is indicative of a deterioration of

the food condition for many marine zooplankters.

An alarming decline in zooplankton population was recorded over the entire area of Tolo Harbour in 1989. Density of zooplankton, averaged over 4 sampling stations, decreased from 52.5 ind.L^{-1} in 1988 to 12.8 ind.L^{-1} in 1989 (Student's *t*-test, $P < 0.001$). Of particular importance was that the decline was observed in both copepods and cladocerans. The number of cyclopoid copepods decreased from 37.49 ind.L^{-1} in 1988 to 8.9 ind.L^{-1} in 1989 (Student's *t*-test, $P < 0.001$). Over same period, the number of calanoid copepods decreased from 11.56 ind.L^{-1} to 5.94 ind.L^{-1} (Student's *t*-test, $P < 0.001$). Equally noticeable decline was found in cladocerans which dropped from an average of 3.45 ind.L^{-1} in 1988 to just 1.45 ind.L^{-1} in 1989 (Student's *t*-test, $P < 0.002$). The suggestion that the decline in zooplankton abundance might be related to dinoflagellate blooms is supported by the observation of an increase in the level of chlorophyll*a* over the same period.

The spatial and temporal occurrences of zooplankton in Tolo Harbour appear to be controlled by many environmental effects. Eutrophication induced phytoplankton bloom and dinoflagellate domination play a very important role on the population dynamics of the zooplankton. The phytoplankton of Tolo Harbour has been studied since the 1970's. Information on long term changes in the abundance and composition of the zooplankton provides better understanding of the impacts of eutrophication in Tolo Harbour and serves as an indicator for changes in water quality.

Chapter 5

Biology of the marine cladoceran *Penilia avirostris* Dana in Tolo Harbour

5.1. Introduction

Cladocerans are small crustaceans which live almost exclusively in freshwater. The abundance of the genus *Daphnia* in the freshwater environment is well known. Of the more than 400 described species of cladocerans, only 8 species were truly marine (Onbé 1977). These belong to the three genera *Evadne, Podon* and *Penilia*. Due to their low species diversity and population size, marine cladocerans have often been viewed as a minor component of the marine zooplankton. In many tropical and warm temperate seas, however, marine cladocerans may constitute an important, and sometimes dominant component of the coastal and near-surface zooplankton (Wickstead 1963; Bosch and Taylor 1968; Onbé 1974, 1978, 1985; Hernoroth and Ackefor 1977; Poggensee and Lenz 1981; Cheng and Chao 1982).

Although many species of marine cladocerans are widely distributed over the oceanic environment (Wiborg 1955; Gieskes 1971; Della Croce and Venugopal 1972; Longhurst and Seibert 1972), dense populations are found mainly in productive coastal waters (Grahame 1976; Moore and Sander 1979).

Population density of marine cladocerans is usually highest in summer and autumn (Yoo and Kim 1987). In fact, the seasonal distribution of many species is characterized by brief occurrence of dense populations in

a particular season, followed by complete disappearance from the zooplankton during the rest of the year (Onbé 1977).

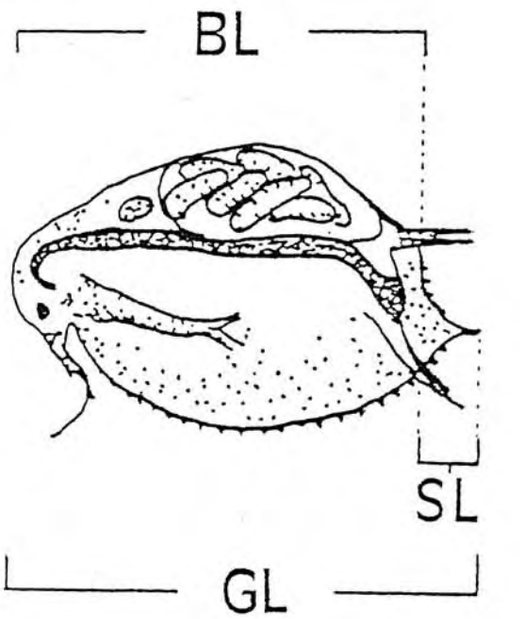
Penilia avirostris Dana is a cosmopolitan marine cladoceran. It occurs most commonly in productive coastal environments and estuaries of the tropics and subtropics (Della Croce and Venugopal 1972; Grahame 1976). In temperate waters, it occurs seasonally in large numbers in productive continental shelf upwellings (Gieskes 1971). The principal mode of reproduction is parthenogenesis. Developing embryos are carried in the brood pouch of the parthenogenetic female and are released as free-swimming miniature adults. Parthenogenesis allows the population to increase very rapidly when environmental conditions are favorable. Although a number of researchers have described the distribution and abundance of *P. avirostris* (Lochhead 1954; Della Croce and Vengopal 1973; Grahame 1976; Yoo and Kim 1987), knowledge on the biology and life history of the species is still limited. This chapter presents some preliminary observations on the morphology and reproduction of *P. avirostris* in Tolo Harbour, Hong Kong.

5.2. Materials and Methods

The hydrography and marine plankton of Tolo Harbour, Hong Kong was sampled at roughly monthly intervals between November 1987 and January 1990. Locations of sampling stations, dates of samplings, and method of zooplankton collection and preservation, are described in Chapter 3. A more intensive survey with weekly sampling was carried out in June and July, 1989.

A total of 818 individuals of *Penilia avirostris* were randomly sorted from zooplankton samples collected in Tolo Harbour between November 1987 and January 1990. Body length and spine length of *P. avirostris* were measured at 40x using a light microscope equipped with an ocular micrometer. Body length was measured from the tip of the head to the dorso-posterior edge of the carapace, and gross length was measured as the length of the whole body from the tip of the head to the end of the shell spine (Fig. 5.1). After length measurement, individual animals were placed on microscope slides and dissected carefully to determine the number of eggs and embryos.

Fig. 5.1 *Penilia avirostris*. BL = Body Length, SL = Shell spine Length, GL = Gross Length.


BL
SL
GL
0.1mm

5.3. Results

Water temperature in Tolo Harbour ranged from 15°C in winter to about 31°C in summer (Fig. 5.2). No seasonal pattern was observed in the population density of *Penilia avirostris* during the study period between November 1988 to February 1989. Correlation between *P. avirostris* density and surface water temperature was poor ($r = 0.02$, $P > 0.1$). Density of *P. avirostris* was never higher than 5 individuals.L^{-1}. The highest density of 4.7 individuals.L^{-1} was recorded in January 1988.

Marked seasonal variations were found in the average body length of *P. avirostris* females (Fig. 5.3). In general, individuals captured during the winter (December, January, February) were larger than individuals captured during the summer (June, July, August) (Student's *t*-test, $P < 0.01$).

Frequency distributions of body length and gross length for *P. avirostris* females are presented in Fig. 5.4. Body length ranged from 0.3 to 1 mm and gross length covered a range from 0.3 to 1.1 mm. The ratio of shell spine length to body length did not vary with body length ($r = 0.03$, $P > 0.1$, $n = 429$), although small individuals appeared to have relatively longer shell spines (Fig. 5.5).

Mean brood size of *P. avirostris* varied seasonally. Although no clear seasonal patterns can be detected (Fig. 5.6), brood size were higher in winter

Fig. 5.2 Density of *Penilia avirostris* with reference to surface water temperature. Each point represents the average value of 4 sampling stations.

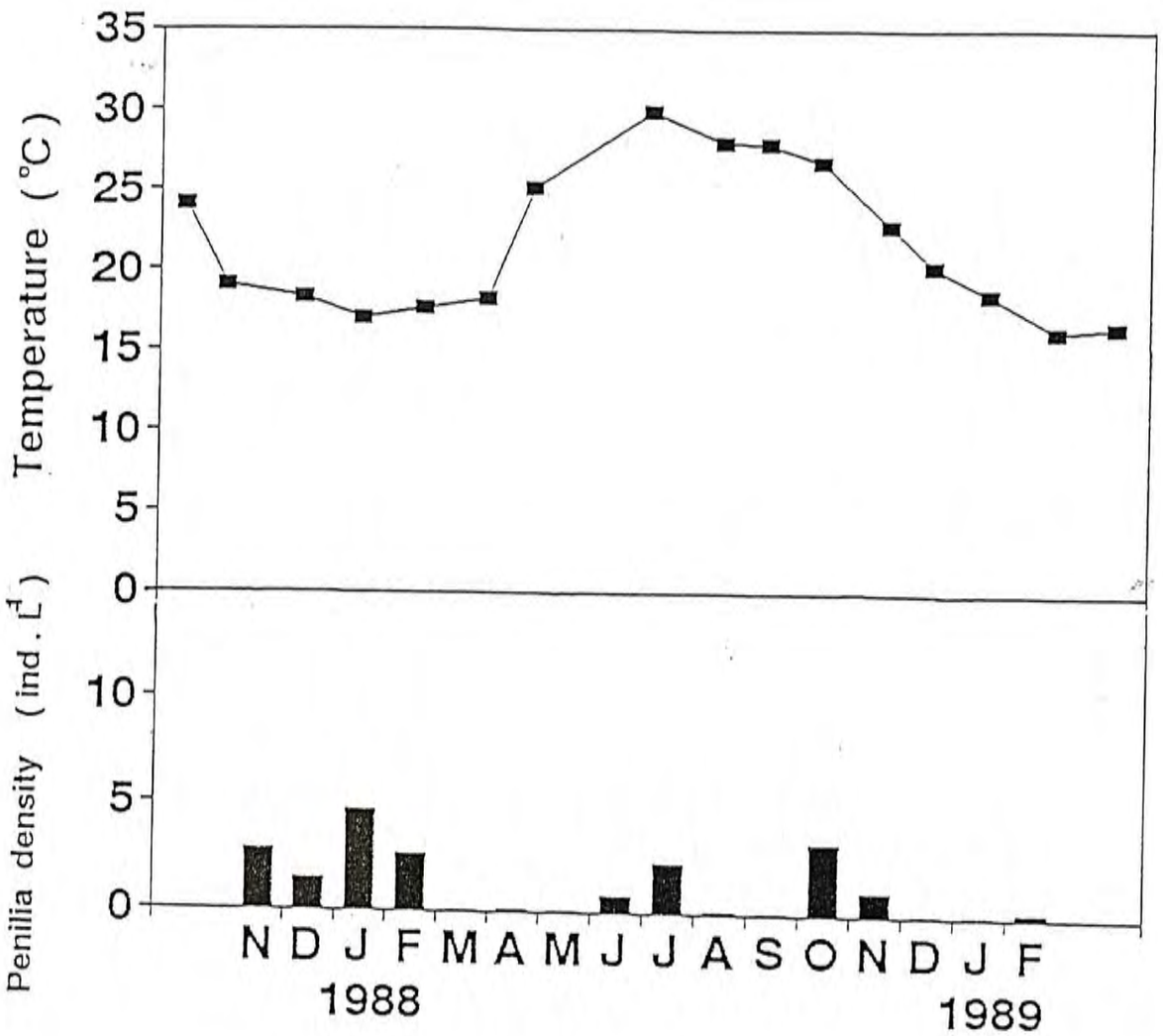

Temperature (°C)
35
30
25
20
15
10
5
0
Penilia density (ind. L-1)
10
5
0
N D J F M A M J J A S O N D J F
1988
1989

Fig. 5.3 Seasonal variation in average body length of *Penilia avirostris* in Tolo Harbour. Each point represents the average of 40 individuals. Vertical bars represent $\pm$ 1 SD.

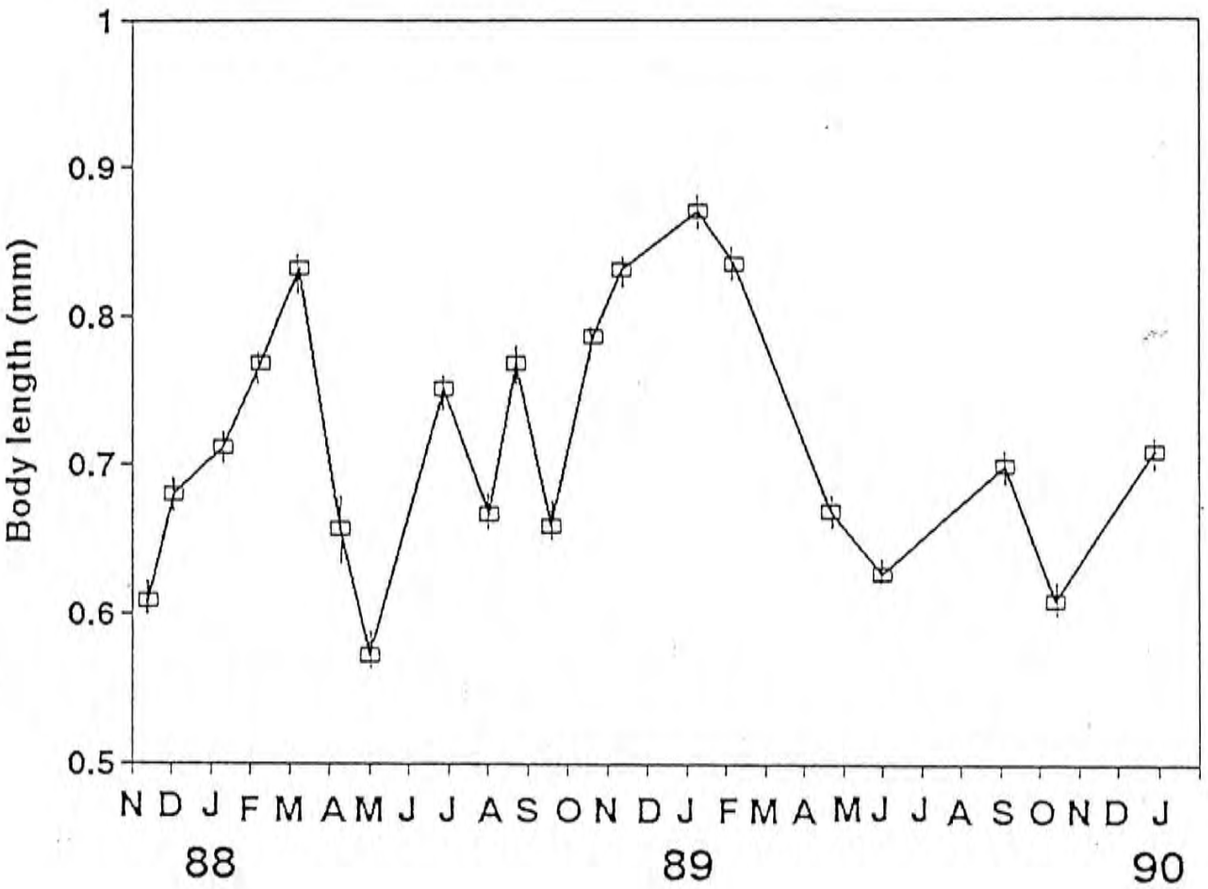
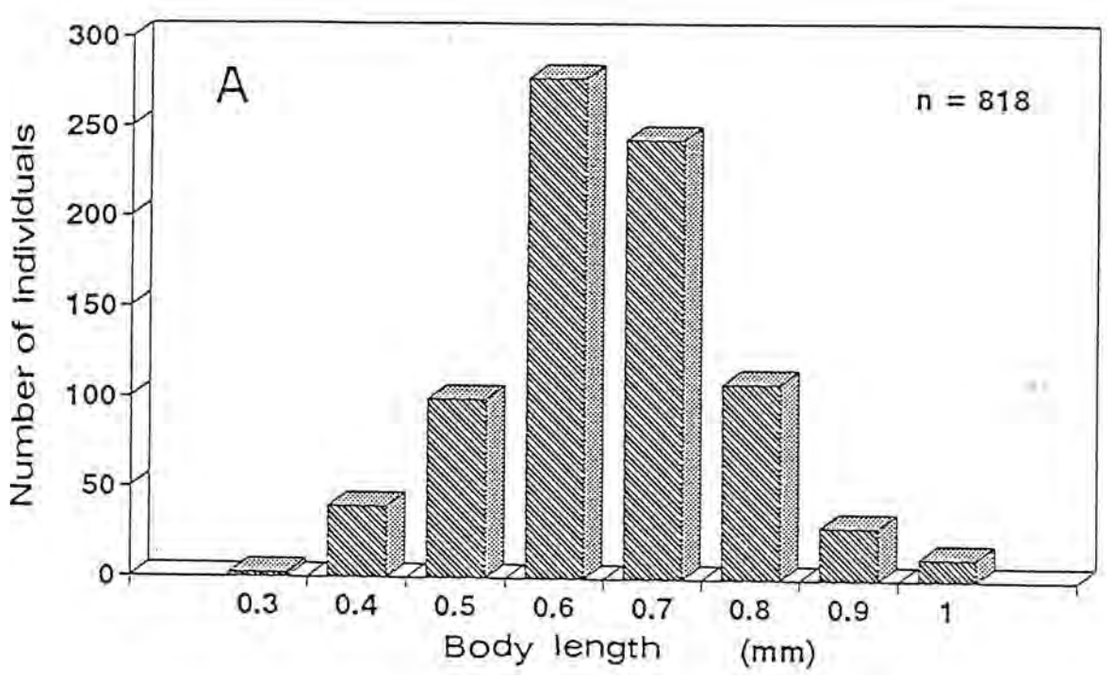

Body length (mm)
1
0.9
0.8
0.7
0.6
0.5
N D J F M A M J J A S O N D J F M A M J J A S O N D J
88
89
90

Fig. 5.4 Frequency distribution of body length (A) and gross length (B) of *Penilia avirostris* in Tolo Harbour.


A
n = 818
Number of Individuals
300
250
200
150
100
50
0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Body length (mm)

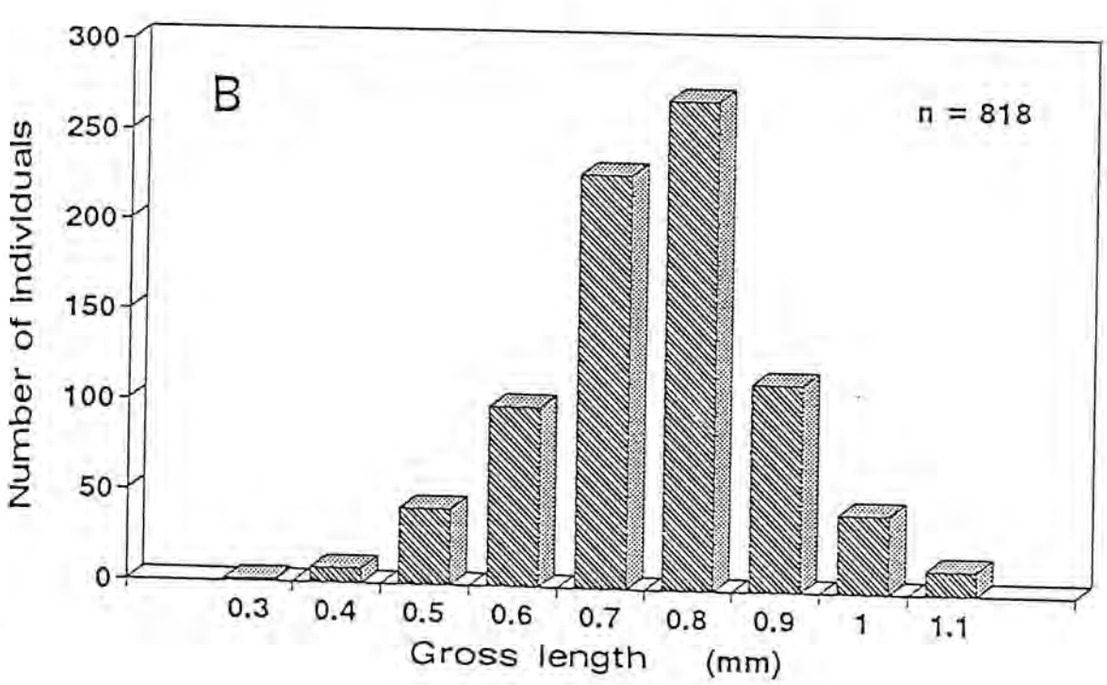

B
n = 818
Number of Individuals
300
250
200
150
100
50
0
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
Gross length (mm)

Fig. 5.5 Relationship between shell spine length to body length ratio and body length of *Penilia avirostris* in Tolo Harbour.

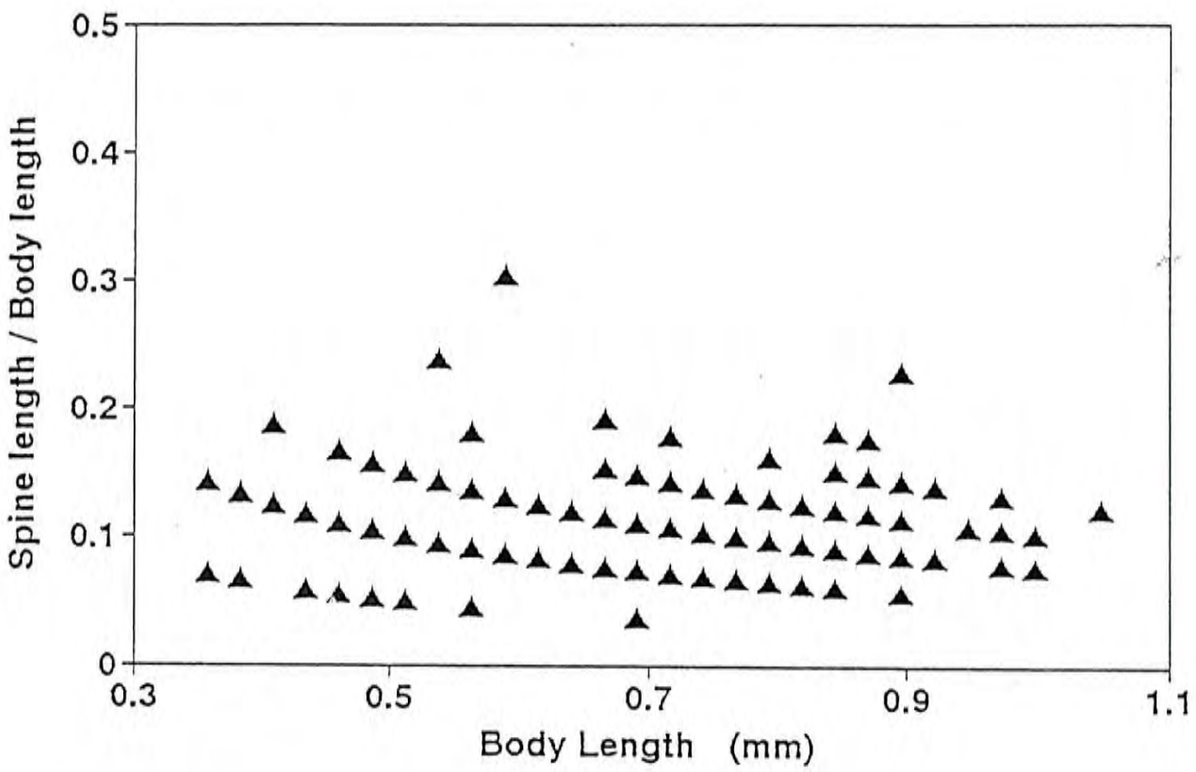
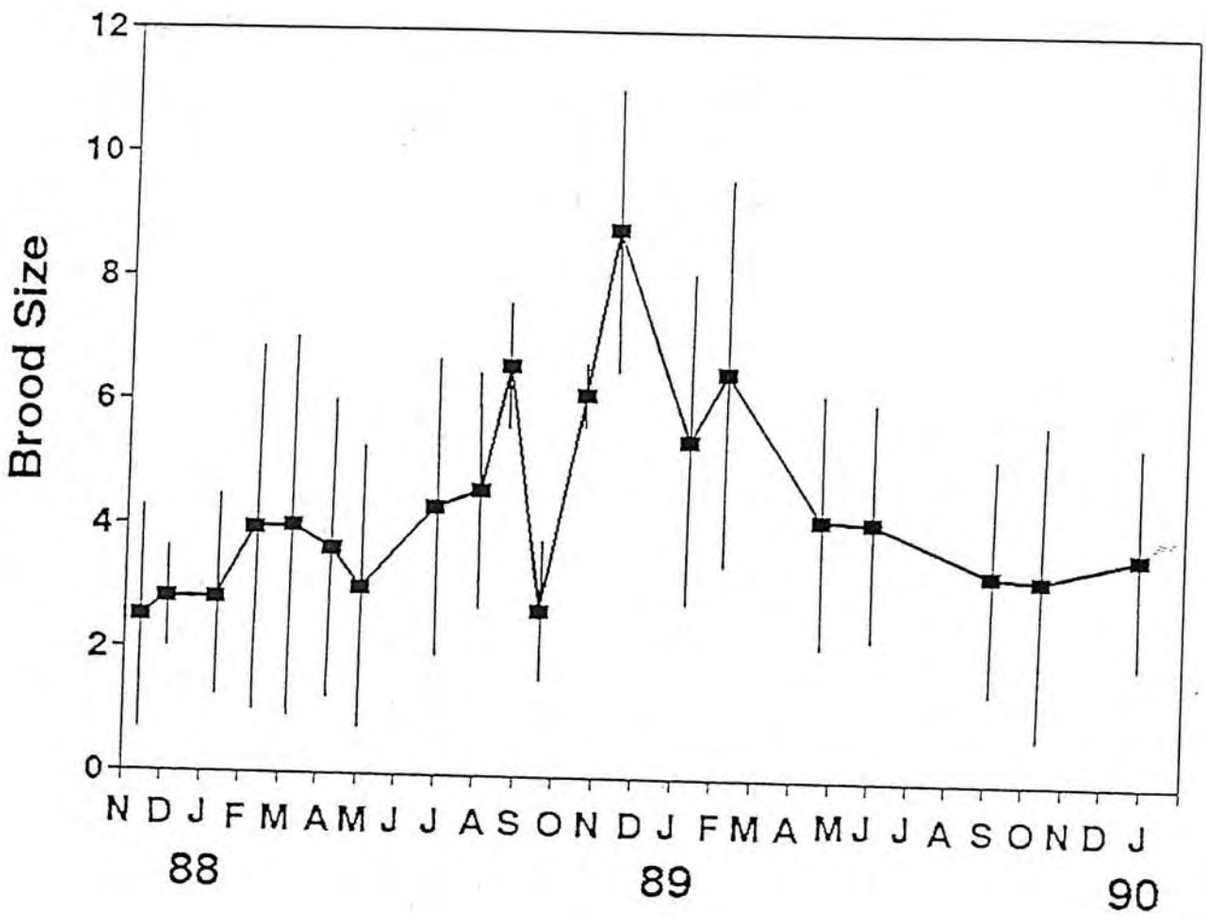

0.5
0.4
0.3
0.2
0.1
0
0.3
0.5
0.7
0.9
1.1
Spine length / Body length
Body Length (mm)

Fig. 5.6 Seasonal changes in mean brood size (mean number of eggs or embryos per female) of *Penilia avirostris* in Tolo Harbour. Vertical bars represent $\pm$ 1 SD.


Brood Size
12
10
8
6
4
2
0
N D J F M A M J J A S O N D J F M A M J J A S O N D J
88
89
90

(December, January, February), than in summer (June, July, August) (Student's *t*-test, $P < 0.025$). Fig. 5.7 shows the frequency distribution of brood size in *P. avirostris* during the period from November 1987 to January 1990. *P. avirostris* carried 1 to 13 eggs or embryos, with a mean of 5.6. A significant positive relationship was found between brood size and body length ($r = 0.55$, $P < 0.001$, $n = 429$) (Fig. 5.8).

The population and reproduction of *P. avirostris* was also studied in a short-term survey in the summer 1989. No substantial changes in water temperature occurred during the study period (Fig. 5.9). Between June 5 to July 10 surface water temperature in Tolo Harbour remained relatively steady at about $20^{o}C$. However, large variation was observed in the number of *P. avirostris*. From a very low level of less than 1 ind.L^{-1} on June 5, the density of *P. avirostris* increased to a maximum of about 13 ind.L^{-1} on June 27, and then declined rapidly to less than 5 ind.L^{-1} on July 10. Correlation between *P. avirostris* density and surface water temperature in the summer survey was also poor ($r = 0.003$, $P >> 0.5$).

A negative relationship between the abundance of *P. avirostris* and their brood size was shown in this survey ($r = 0.6$, $P < 0.001$). Average brood size was smallest on June 27 when population density was at the highest level. No changes in the average body length of *P. avirostris* were observed during the same period (Fig.5. 10).

Fig. 5.7 Frequency distribution of number of eggs or embryos per female for *Penilia avirostris* in Tolo Harbour.

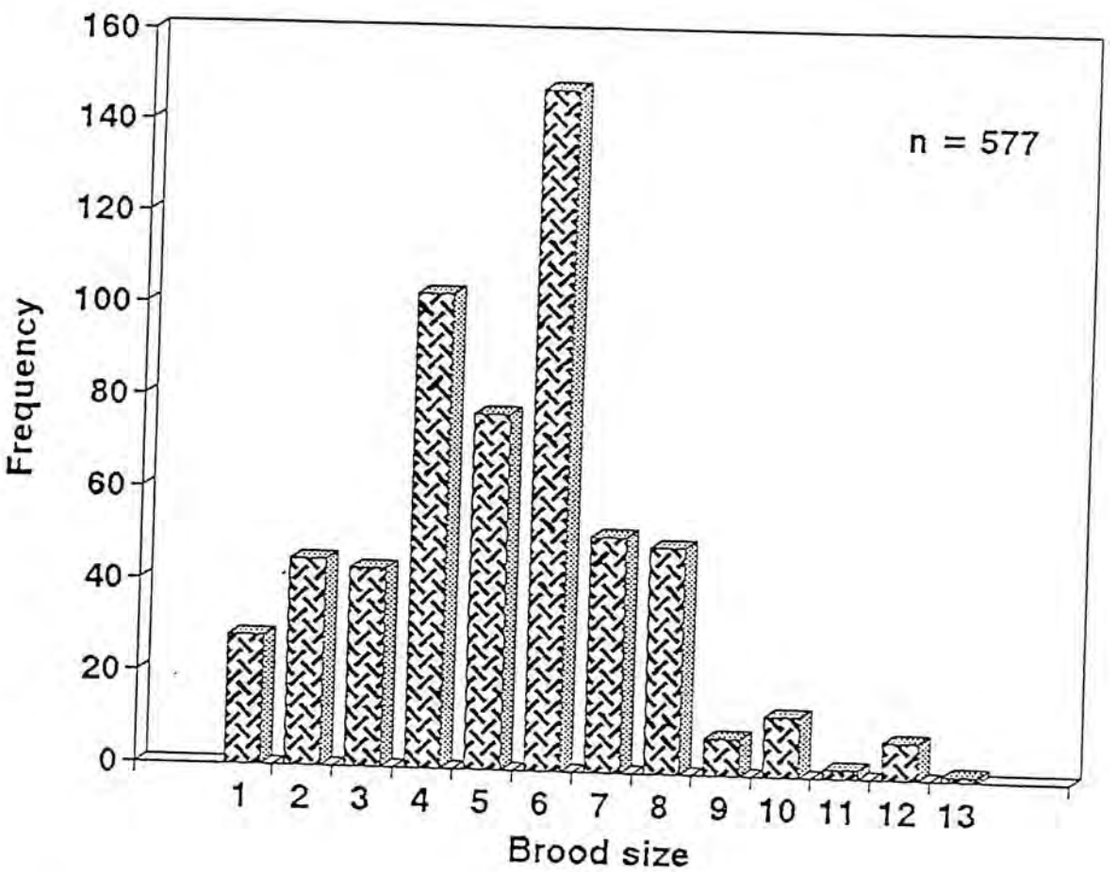

160
140
120
100
80
60
40
20
0
Frequency
n = 577
1
2
3
4
5
6
7
8
9
10
11
12
13
Brood size

Fig. 5.8 Relationship between brood size and body length for *Penilia avirostris* in Tolo Harbour.

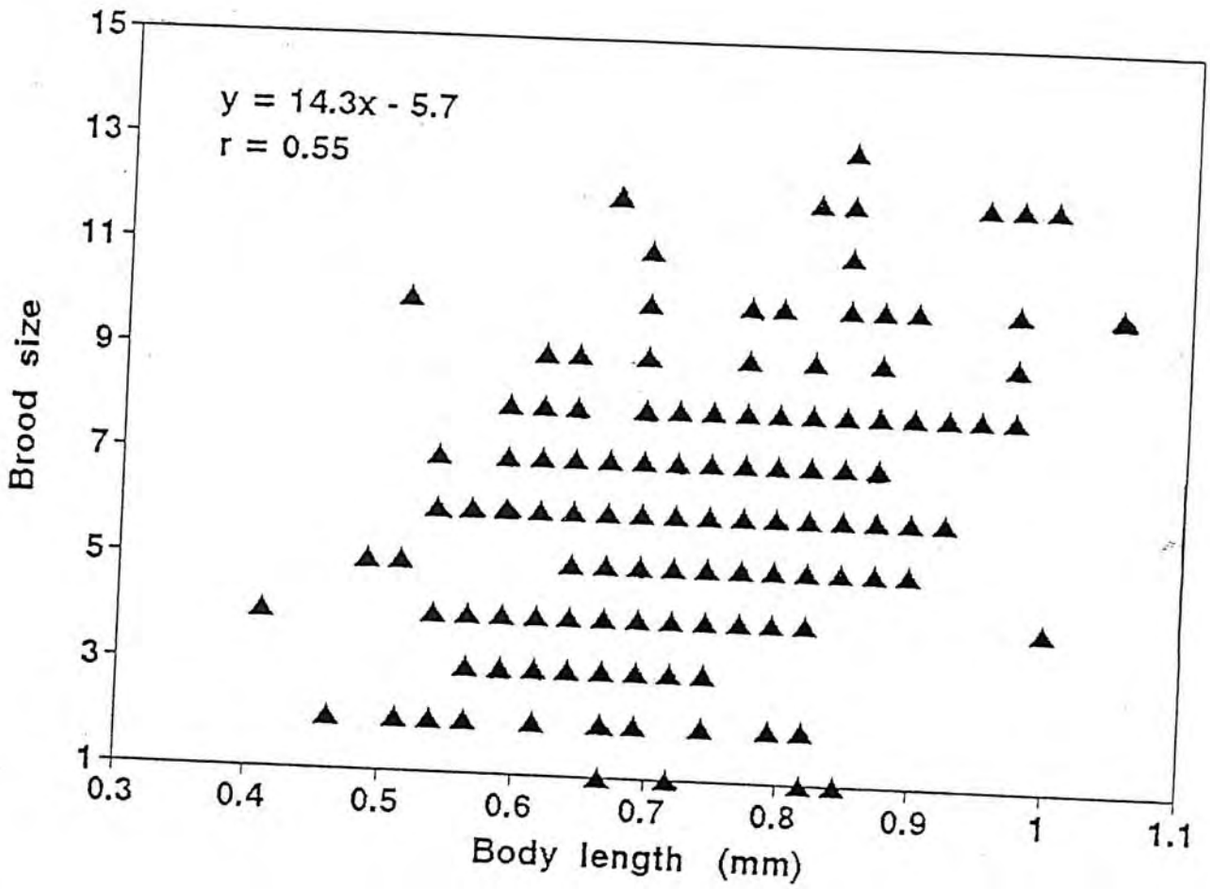

y = 14.3x - 5.7
r = 0.55
Brood size
15
13
11
9
7
5
3
1
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
Body length (mm)

Fig. 5.9 Density of *Penilia avirostris* with reference to surface water temperature during June and July 1989. Each point represents the average value of 4 sampling stations.

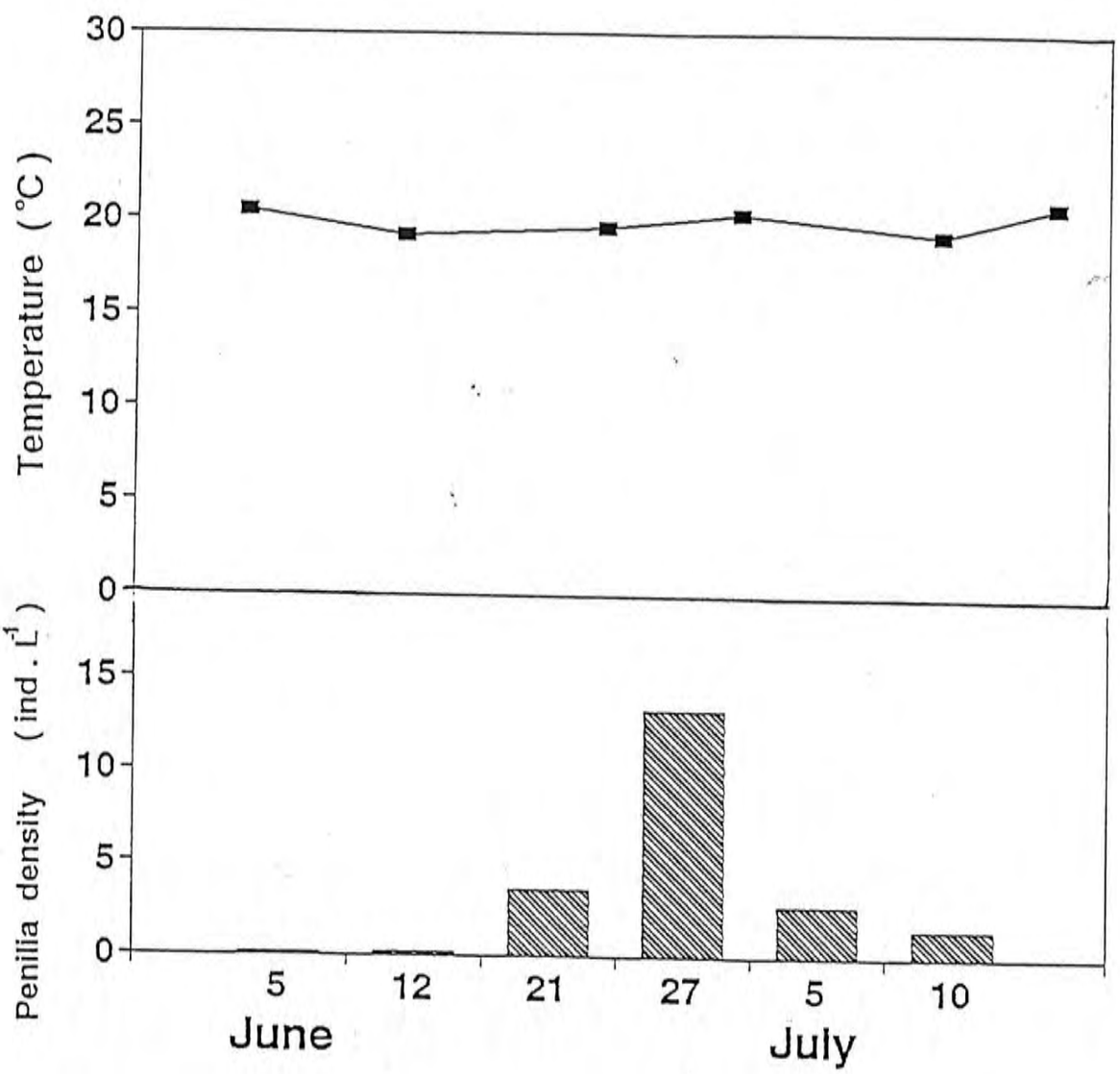
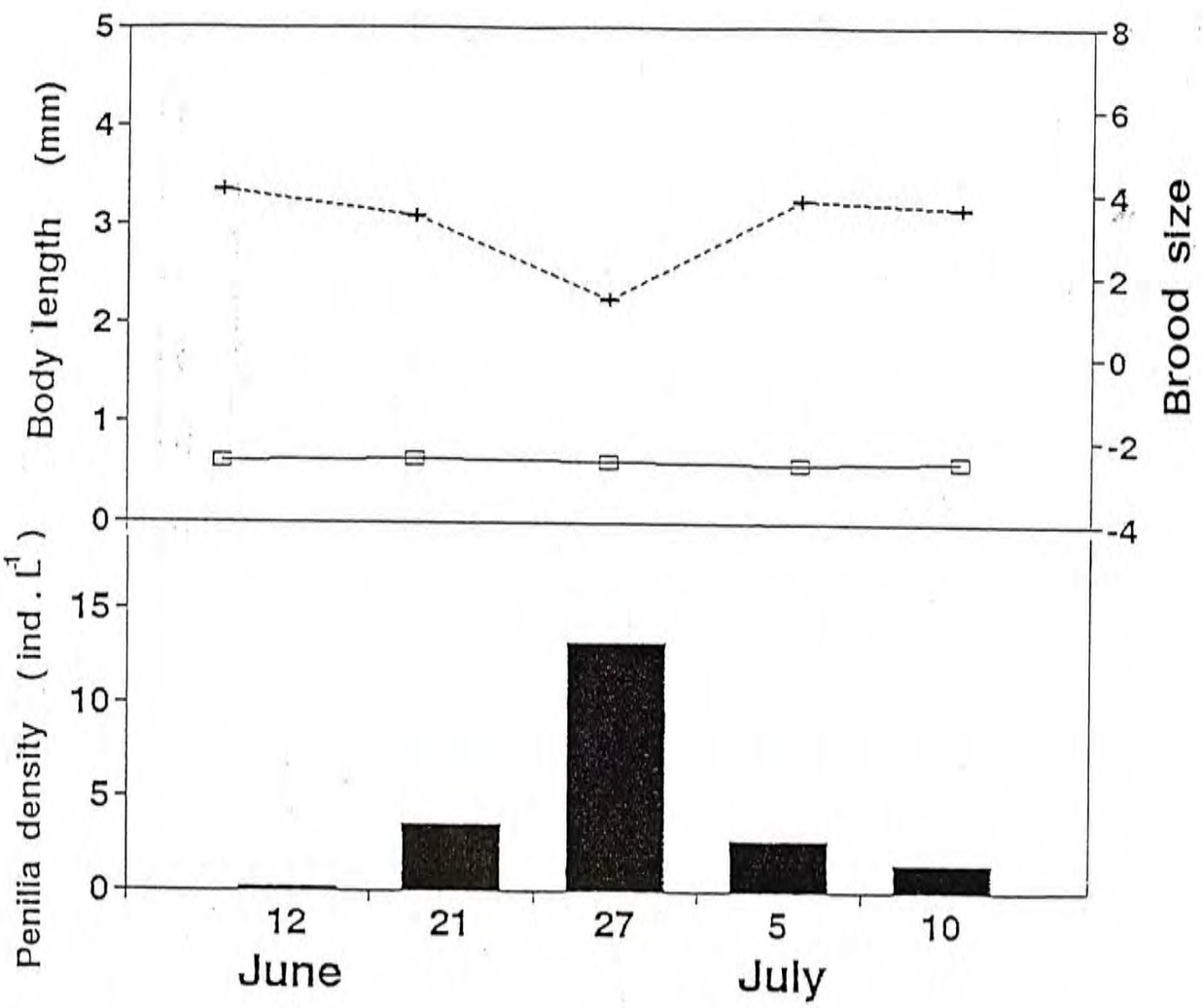

30
25
20
15
10
5
0
Temperature (°C)
15
10
5
0
Penilia density (ind. L-1)
5
12
21
27
5
10
June
July

Fig. 5.10 Body length (—⊟—), brood size (·-+-·) and population density of *Penilia avirostris* in Tolo Harbour during June and July 1989.


Body length (mm)
Brood size
Penilia density (ind . L-1)
5
4
3
2
1
0
8
6
4
2
0
-2
-4
15
10
5
0
12
21
27
5
10
June
July

5.4. Discussion

The number of *Penilia avirostris* in Tolo Harbour fluctuated widely throughout the study period, but no clear seasonal pattern of occurrence was observed. Occurrence of marine cladocerans in temperate oceans is mostly limited to the warmer seasons (Hirota 1968; Onbé 1977; Yoo and Kim 1987). In contrast, in tropical and subtropical waters, many marine cladocerans occur throughout the year (Pillai and Pillai 1975; Cheng and Chao 1982). Della Croce and Venugopal (1973) found that *P. avirostris* occurs in temperatures ranging from 8.7- 31^{o}C. The ability of *P. avirostris* to survive in low temperature was confirmed by Yoo and Kim (1987) who reported *P. avirostris* at water temperatures below 10^{o}C. In Tolo Harbour water temperature ranged from 15^{o}C in winter to about 31 ^{o}C in summer, and no correlation was found between surface water temperature and number of *P. avirostris*. Presence of dense populations in the winter suggests that the occurrence of *P. avirostris* is not restricted to the warmer seasons in subtropical Hong Kong waters.

Kim *et al.* (1989) found that the seasonal occurrence of the marine cladoceran *Podon schmackeri* is related to both water temperature and food levels. Although *P. avirostris* are most abundant in productive inshore waters, Paffenhöfer and Orcutt (1986) pointed out that it is well adapted to the low food levels of oligotrophic oceanic waters. In the highly eutrophic conditions of Tolo Harbour, it is reasonable to assume that no food deficiency occurred for the *P. avirostris* even during the winter.

The principal mode of reproduction in *P. avirostris* is parthenogenesis. The high reproductive potential of parthenogenetic life strategy allows *P. avirostris* populations to increases rapidly when conditions are favorable. In most cladocerans, the number of youngs in a brood depends upon the size of the female (Hebert 1978). Similarly, a significant positive relationship exists between body length and brood size in *P. avirostris*. Onbé (1977) pointed out that the size of parthenogenetic females increases with the growth of the embryos. Fully developed embryos are released into the water upon the moulting of the mother. Kim *et al.* (1989) also noted that parthenogenetic females carrying advanced embryos at the point of release show sudden reduction in the size of the brood pouch when the embryos were discharged.

A special type of parthenogenesis known as paedogenesis occurs in some marine cladocerans. Paedogenesis was first observed in *Evadne nordmanni* as early as 1911 by O. Kuttner (cited in Onbé 1977). Advanced embryos of *E. nordmanni* which have developed within the brood pouch of parthenogenetic females are often found to carry their own eggs in their embryonic brood space. These embryos develop further and, by the time they are released from the brood pouch of their mother as free-swimming females, their own eggs have already reached a blastula stage with a large cleavage cavity. Bainbridge (1958) called these young females miniature adults. The phenomenon of paedogenesis appears to be confined to species of Polyphemoidea (Mordukhai-Boltovskoi and River 1971; Bosch and

Taylor 1973; Onbé 1974). Paedogenesis has not been reported in species of Sidoidea and was not observed in individual specimens of *P. avirostris* examined in this study.

Studies over the past century (Coker and Addlestone 1938; Brooks 1947; Jacobs 1961; Dodson 1974) have revealed that many species of freshwater cladocerans exhibit cyclomorphosis or seasonal changes in body shape. Cyclomorphosis often involves a dorso-anterior expansion of the head which produces a laminate crest, a reduction in body width, and an increase in the length of the shell spine. No evidence of cyclomorphosis was observed in *P. avirostris* during this study. An one-way ANOVA with month as the main effect reveals no seasonal variations in the ratios of spine length to body length ($P > 0.1$). In contrast, significant monthly variations were found in both body length (1-way ANOVA, $P << 0.0005$) and brood size (1-way ANOVA, $P < 0.0005$) of *P. avirostris*. In general, both body length and brood size appear to increase during the winter.

Parthenogenetic females of *P. avirostris* in Tolo Harbour ranged from 0.3-1.0 mm in body length and 0.3-1.1 mm in gross length. Body lengths showed great seasonal variations. Individuals were smaller in summer and larger during winter. Hebert (1978) pointed out that the maximum size reached by cladocerans is often related to food supply. When food supply is low, adults cease growth on reaching maturity and acquire shorter carapace length. In contrast, when food is abundant, growth continues throughout life. Chlorophyll*a* concentrations in Tolo Harbour exhibit no seasonal patterns. In addition, despite the eutrophic conditions in Tolo Harbour, the

phytoplankton is frequently dominated by dinoflagellates which are not suitable food for *P. avirostris* (Kim *et al.* 1988). And also, red tide occurrence in Tolo Harbour is more common in summer than the rest of the year (E.P.D. 1989, 1990). These observations supports that reduction in the body length during the summer may be related to nutrient deficiency.

The occurrence of smaller-sized *P. avirostris* in the summer may also be related to size-selective predation by fish. Brooks and Dodson (1965) proposed that the introduction of visual predators such as fish into lakes and ponds may shift the size distribution of zooplankton towards smaller species. By analyzing gut contents, Galbraith (1967) was able to confirm that fish consumed a disproportionate number of the larger zooplankton. Since the number of small planktivorous fish is usually highest in spring and early summer (Walsh *et al.* 1980), a smaller body size would reduce the susceptibility of *P. avirostris* to fish predation.

The brood size of *P. avirostris* fell to very low levels when population densities were high. Figure 5.10 shows that the abundance of *P. avirostris* increased from 3.6 individuals.L^{-1} to 13.2 individuals.L^{-1} between 21 June and 27 June, and then declined rapidly within a few days to less than 3 individuals.L^{-1}. During the same period, average number of embryo per female decreased from 3.4 on 21 June to 1.3 on 27 June, and then increased to 3.8 on 5 July. Paffenhöfer and Orcutt (1986) observed that the generation time of *P. avirostris* was about 6 days under favorable food conditions. Sudden changes in the population density and brood size of

P. avirostris in Tolo Harbour confirm that parthenogenesis and short generation time are adaptations for high rates of population increase when environmental conditions are favorable.

Fluctuations in the brood size of *P. avirostris* may reflect changes in food density (Bainbridge 1958). The pattern in Tolo Harbour consists of low population in the spring with large mean brood size and temporarily high population density in the summer with much lower egg production. Brooks (1946) suggested that the mid-summer reduction in brood size of *Daphnia* was a consequence of temperature change rather than food depletion because algae were still abundance. However, it is now known that common summer algae such as the blue-greens are poor sources of food for *Daphnia* (Schindler 1970; Arnold 1971). Other experiments have also revealed that temperature plays a relatively minor role in determining brood size. Hall (1964), for example, found similar maximum brood sizes for *D. galeata* cultured over a range of temperature from 15 to 25^{o}C. In Tolo Harbour, increase dominance of dinoflagellates have probably reduced the amount of edible food for *P. avirostris* during the summer, and the decline in brood size could be the result of food depletion.

Chapter 6

Grazing Behaviour of the marine cladoceran *Penilia avirostris* Dana in Tolo Harbour

6.1. Introduction

Penilia avirostris occurs most commonly in productive near- and in-shore waters of the subtropics and tropics (Pavlova 1959a; Della Croce and Venugopal 1973; Grahame 1976; Moore and Sander 1979). Although Paffenhöfer and Orcutt (1986) reported that *P. avirostris* is well adapted to the low food level of oligotrophic open oceanic waters, the frequent association of *P. avirostris* with productive nearshore waters, polluted bays and estuaries (Kiortsis and Moraitou-Apostolopoulou 1975; Grahame 1976; Moore and Sander 1979) suggests that *P. avirostris* may be food limited in the open sea.

Information on the feeding habits of marine cladocerans is limited. Some Soviet investigators reported that *P. avirostris* prefers bacteria and small flagellates with particle size less then of 8 µm (Pavlova 1959; Sorokin *et al.* 1970). Gore (1980) found that although *P. avirostris* can ingest particles of up to 50 µm, it prefers particles smaller than 20 µm. The particle size range which can be ingested by marine cladocerans is not well known. Lochhead (1936) studied the feeding mechanisms of *P. avirostris* and reported several ways by which the animals can avoid clogging of the feeding appendages by particles smaller than 8 µm. More recently, Turner *et al.* (1988) reported that *P. avirostris* did not ingest free-living bacterioplankton, but preferred large or aggregated bacteria. In addition, these authors demonstrated food selectivity in *P. avirostris* by showing that chain-forming

diatoms, large diatoms and the dinoflagellates *Pseudoisochrysis paradoxa* (5-6 μm) were not ingested, but the diatoms *Thalassiosira pseudonana* (4-6 μm) and *Thalassiosira weissflogii* (10-12 μm) were. When *P. avirostris* was offered natural particulate assemblages as food, ingestion maxima occurred for particles between about 4- and 6- μm equivalent spherical diameter. The results of Turner *et al.* (1988) suggest the *P. avirostris* is not necessarily bacterivorous. Kim *et al.* (1988) also found that diatoms such as *Skeletonema costatum, Cyclotella meneghiniana, Thalassiosira* sp., *Coscinodiscus* sp. and *Chaetoceros* sp. were the main food source for marine cladocerans in the Inland Sea of Japan.

Previous laboratory studies have shown that factors such as temperature, food concentration, hunger, food quality and food size can affect the feeding behaviour of zooplankters (reviewed by Conover and Huntley 1980; Frost 1980). Although many laboratory feeding experiments have been conducted, most have limited predictive value for natural situations. The aim of this study was to investigate the *in situ* feeding rate of *P. avirostris* by means of the gut fluorescence method (Mackas and Bohrer 1976; Dagg and Wyman 1983). Gut evacuation rate was measured in the laboratory, and ingestion rates were calculated from measurements of gut pigment content and gut evacuation rate. Comparison was made between the feeding rates of *P. avirostris* in the laboratory and the natural environment. Ingestion rate data combined with estimates of *in situ* chlorophyll*a* concentration and estimates of *P. avirostris* abundance were used to estimate the feeding impact of *P. avirostris* in Tolo Harbour.

6.2. Materials and Methods

6.2.1. Isolation of algae from Tolo Harbour

0.1 mL of surface water from Tolo Harbour was serially diluted with 0.9 mL sterilized sea water. 0.1 mL of the diluted solution was plated on agar plates containing Walne's Medium (Walne 1966). The plates were incubated in a growth chamber at 22-25 ^{o}C and illuminated by fluorescent lamps with a 16:8 LD cycle (Wong 1979). Successfully isolated colonies were streaked progressively onto new plates to maintain the algal culture. *Chlorella ellipsoidea* and *Chlorella pyrenoidosa* were successful isolated by this method from surface water collected in Tolo Harbour.

Skeletonema costatum was isolated in a different way. Water samples collected from Tolo Harbour during a red tide occurrence was examined under a microscope. Single colonies were taken out with a micro-pipette and transferred to Walne's Medium for incubation.

6.2.2. Algal culture

Five strains of green algae (*Isochrysis* aff. *galbana, Platymonas* sp., *Nannachloris oculata, Chlorella ellipsoidea* and *Chlorella pyrenoidosa*) and three strains of diatoms (*Chaetoceros gracilis, C. minus* and *Skeletonema costatum*) were used for laboratory feeding experiments. *S. costatum* and

the 2 species of *Chlorella* were isolated from surface water samples collected in Tolo Harbour. The other algae came from stock cultures maintained in the laboratory of Dr. K.H. Chu (The Chinese University of Hong Kong).

Stock cultures of these algal species were kept on agar slants containing 2% agar in Walne's Medium (Walne 1966) and place under constant temperature at 25 ^{o}C and dim light conditions (Wong 1979). The cultures were incubated using techniques similar to those described by Wong (1979). 5% (V:V) inoculum of actively growing algal cells were inoculated to 190 mL Walne's Medium in Erlenmyer flasks. Volume of the growth medium did not exceed two-fifths that of the flask to ensure adequate light penetration and aeration. The flasks were then placed in a growth chamber at 22-25 ^{o}C and illumination by fluorescent lamps with a 16:8 LD cycle.

6.2.3. Measurement of gut content

Twenty *Penilia avirostris* individuals picked under a dissecting microscope were placed into a glass tube with 5 mL 90% acetone and stored in darkness at 4 ^{o}C for 24 h. Fluorescence of the acetone extract was measured before and after acidification (3.3×10^{-3} M HCL) with a Turner Model-112 fluorometer. Gut content (ng pigment.ind^{-1}), the total amount of pigment (chlorophyll*a* + phaeopigment) in each animal was calculated using the equations of Dagg (1983):

$$\text{Chlorophyll}a\ (\text{ng.ind}^{-1}) = K\,(F_o - F_a).N^{-1}.V^{-1} \qquad (1)$$

$$\text{Phaeopigment (ng.ind}^{-1}) = K\,(RF_a - F_o).N^{-1}.V^{-1} \qquad (2)$$

where K is an instrument calibration constant, F_o and F_a are the fluorescence readings before and after acidification, N is the number of animals, V is the volume of the acetone extract in units of mL and R is the acidification ratio.

6.2.4. Measurement of gut evacuation rate

Several hundred *P. avirostris* collected from Tolo Harbour were acclimatized for 1 to 2 h in large aquaria (> 10 L) containing surface water from Tolo Harbour at about 21° C. Algae, concentrated from surface water from Tolo Harbour by filtration, were added to the aquaria to obtain a final chlorophyll*a* concentration of approximately 300 ng.mL^{-1} or 1.0 x 10^5 cells.mL^{-1}. After 3 h, animals were gently collected on a 0.125 mm mesh, rinsed with filtered (0.45 µm) seawater and transferred immediately into 3-L glass beakers containing filtered (0.45 µm) seawater. Animals were collected periodically for 3 h by pouring 200 mL samples through a 125-mm mesh. Animals collected on the mesh were frozen immediately and processed as described above for gut pigment content analysis. Gut evacuation rate was calculated from the equation :

$$G_t = G_0 e \qquad (3)$$

where G_t is the amount of pigment in the gut at time t, G_0 is the pigment at the beginning of the measurement period, k is the gut evacuation rate in units of min^{-1}, and t is the time in min.

6.2.5. Measurement of ingestion rate and clearance rate

Ingestion rate (I) of *P. avirostris* was calculated as follows:

$$I = kG \qquad (4)$$

with unit of I = ng pigment.individual^{-1}.min^{-1}.

Clearance rates (F) in units of mL.individual^{-1}.min^{-1} was calculated from the relationship:

$$F = I.C^{-1} \qquad (5)$$

where C is the *in situ* chlorophyll*a* concentration measured in units of ng chl*a*.mL^{-1}.

6.2.6. Feeding impact

Feeding impact by *P. avirostris* (P), expressed as the total volume of water (mL) swept clear per litre of volume per day, was calculated from the relationship:

$$P = AF' \quad (6)$$

where A = number of *P. avirostris*.L^{-1}. F'= clearance rate converted to units of mL.individual^{-1}.day^{-1} from the relationship :

$$F' = F(60)(24) \quad (7)$$

6.2.7. Laboratory feeding experiments

Diel variation in gut content of *P. avirostris* was measured in 1000-L cylindrical (1.1 m diameter) fibreglass outdoor tanks containing the natural assemblage of zooplankton from Tolo Harbour. Animals were collected from vertical net hauls and used within 48 h of capture. Density in experimental tanks was maintained at about 10 animals.L^{-1}. Surface seawater in the tanks was enriched with either *Chaetoceros gracilis* or *Nannachloris oculata*. Measured volume of cultered phytoplankton were added to the tanks to provide final food concentrations of 100 ng Chl*a*.mL^{-1} ($\sim 0.3 \times 10^5$ cells.ml^{-1}) for experiments with *C. gracilis* and 30 ng chl*a*.mL^{-1} ($\sim 2.0 \times 10^5$ cells.ml^{-1}) for experiments with *N. oculata*. Seawater in the

tanks were gently aerated to keep the algae and animals in suspension. All experiments were set up in duplicate. Temperature during experiment ranged from 18-25 ^{O}C, and salinity ranged from 33 ppt - 35 ppt. Animals in the tank were sampled periodically for 24-36 h by hauling a small conical net (0.25 m mouth diameter) from bottom to surface. Gut pigment contents of the animals were measured fluoremetrically. Seawater samples taken from the surface and bottom of the tanks at the end of the experiment and tested for chlorophyll*a* concentration suggested that algae in the tanks were distributed evenly.

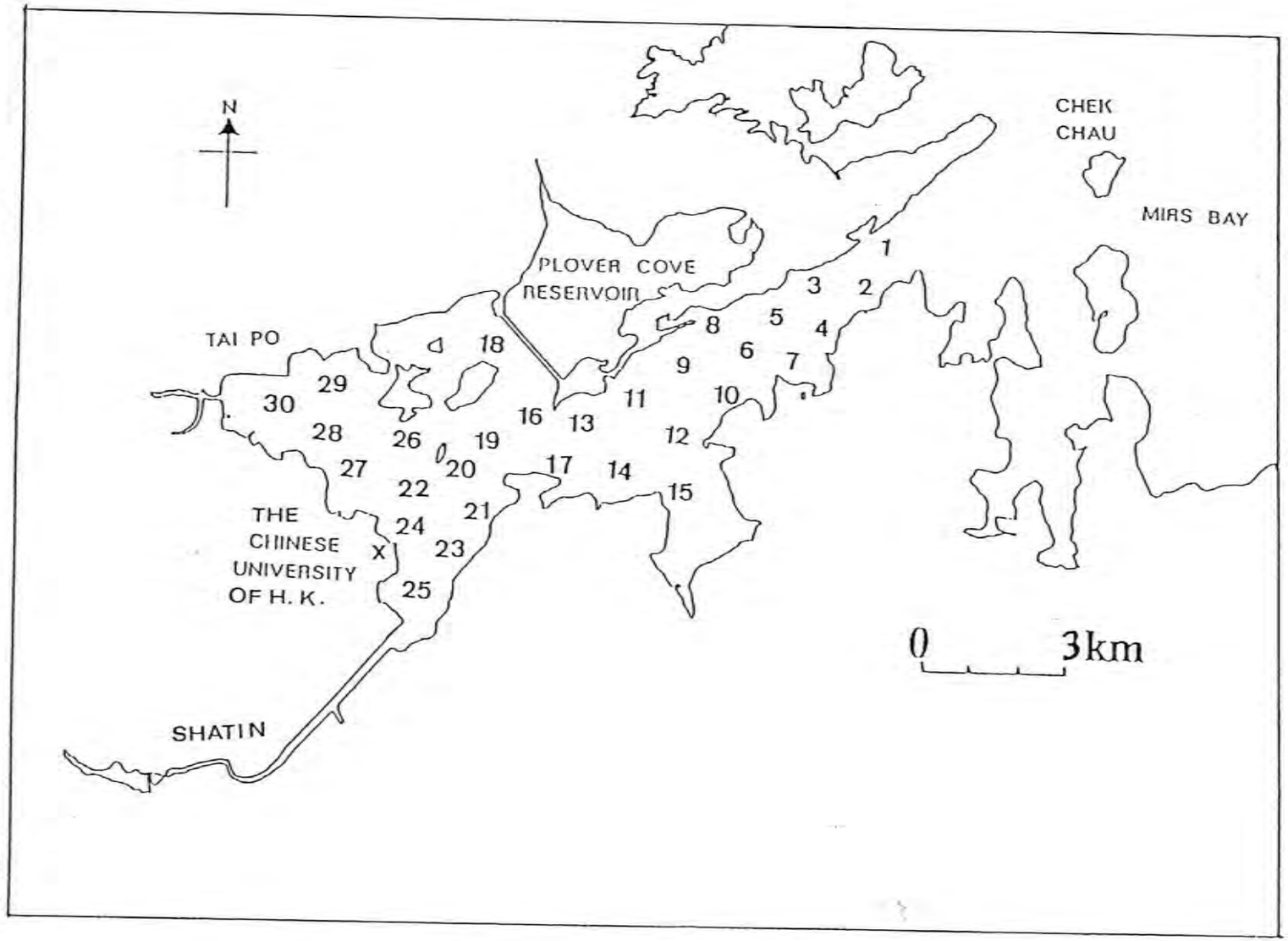
Feeding behaviour of *P. avirostris* on 8 strains of phytoplankton was studied in the laboratory. Food media were prepared by adding aliquots of algae to 0.45 µm filter-sterilized surface seawater. Experiments were performed in 50 mL glass vials containing 40 mL of food medium. Experiments began when 20 *P. avirostris* were added to each vial. Vials were placed in the dark at 20 ^{O}C. Experiments lasted 3 - 4 h. Contents of the vials were not stirred, but sedimentation of algae was negligible. At the end of each experiment, contents of the vial were poured through a 0.125 mm mesh to collect the animals for gut pigment content analysis. Five replicates were used for each food concentration.

6.2.8. *In situ* experiment

Experiments were conducted in June 1989 and in November 1989

during a red tide bloom. On the day of the experiment, animals were collected at 30 locations in Tolo Harbour (Fig. 6.1) between 0900 h and 1300 h by hauling a 0.125 mm mesh plankton net vertically from bottom to surface. Contents of the net haul were filtered through a 0.125 mm mesh netting, and animals retained on the nets were rinsed with filtered sea water. About half of animals from each net haul were immediately frozen. The other half of the captured animals was kept in natural sea water and brought to the laboratory for feeding experiments described earlier. Zooplankton density and chlorophyll*a* concentration at each location were measured using methods described in Chapter 3.

Fig. 6.1 Map of Tolo Harbour showing location of the 30 sampling sites.


N
CHEK
CHAU
MIRS BAY
PLOVER COVE
RESERVOIR
TAI PO
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
THE
CHINESE
UNIVERSITY
OF H. K.
SHATIN
0
3km

6.3. Results

6.3.1. Indoor experiments

When *Penilia avirostris* were transferred from a food medium containing 1 x 10^5 cells.mL^{-1} to 0.45-μm filtered seawater, their gut fullness declined rapidly. Following studies of gut evacuation in copepods (Mackas and Bohrer 1976; Dagg and Grill 1980; Dagg and Wyman 1983), the time course of decline in gut fullness was described by an exponential equation (Fig. 6.2). Gut fullness declined most rapidly during the first hour such that only a very small amount of phytoplankton pigments remained in the gut after 2 h. Gut evacuation rate was 2.2 % min^{-1}.

P. avirostris fed *Chaetoceros gracilis* (Fig. 6.3) and *N. oculata* (Fig. 6.4) showed pronounced diel variations in gut pigment content. Gut pigment content was low (~ 0.5 ng pigment.ind^{-1}) during daylight hours, then began to rise around sunset (1830 h). For *P. avirostris* fed *C. gracilis*, gut pigment content reached a peak of about 1.5 ng pigment.ind^{-1} at midnight and then declined rapidly to about daytime level at sunrise (0530h). Similarly, gut pigment contents of *P. avirostris* fed *N. oculata* were highest at around midnight and returned to very low level shortly after sunrise. In general, gut pigment content of both groups of *P. avirostris* began to decline before sunrise and reached daytime values by 0600h. From morning through afternoon, gut pigment content remained fairly constant or declined slightly.

Fig. 6.2 Rate of gut evacuation by *Penilia avirostris* at 20^{O}C.

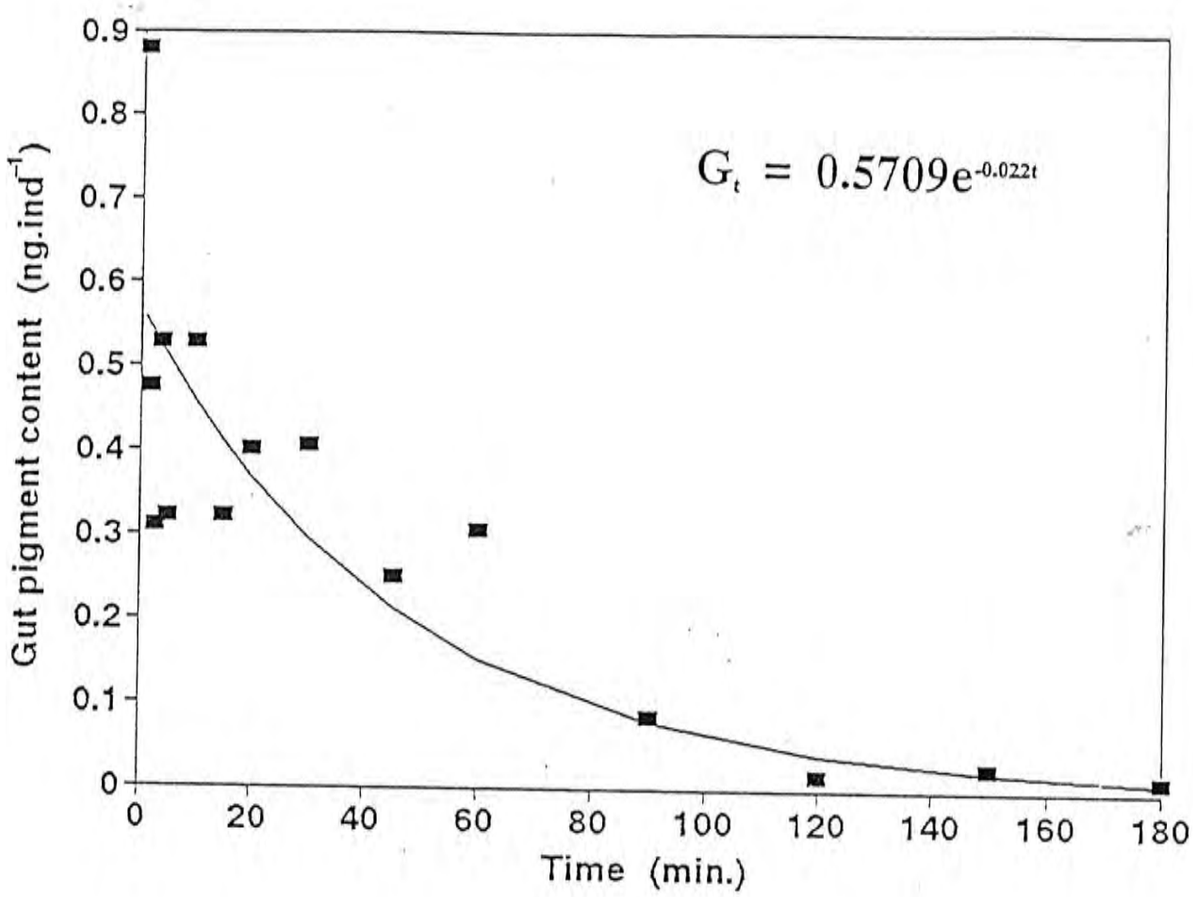

$G_t = 0.5709e^{-0.022t}$
Gut pigment content (ng.ind^{-1})
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
20
40
60
80
100
120
140
160
180
Time (min.)

Fig. 6.3 Diel variation of gut pigment content (A), ingestion rate (B) and clearance rate (C) for *Penilia avirostris*. Experiment was carried out on July 17 - July 18, 1990. Times of sunset (SS) and sunrise (SR) were 1830 h and 0530 h. Animals fed *Chaetoceros gracilis* at 100 ng Chl*a*.mL^{-1}. Each point represents the average of 2 fluorometer counts using a total of 40 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

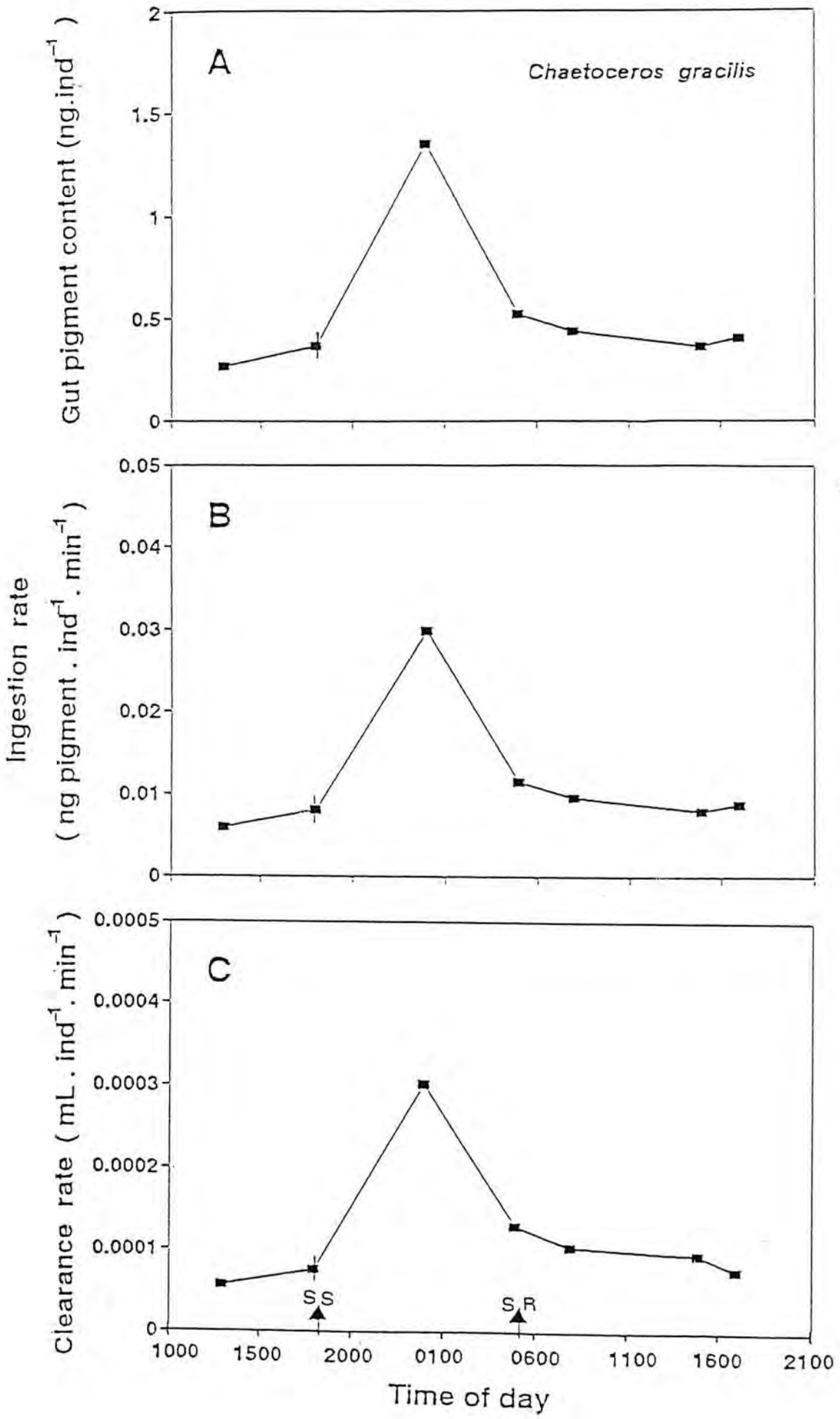
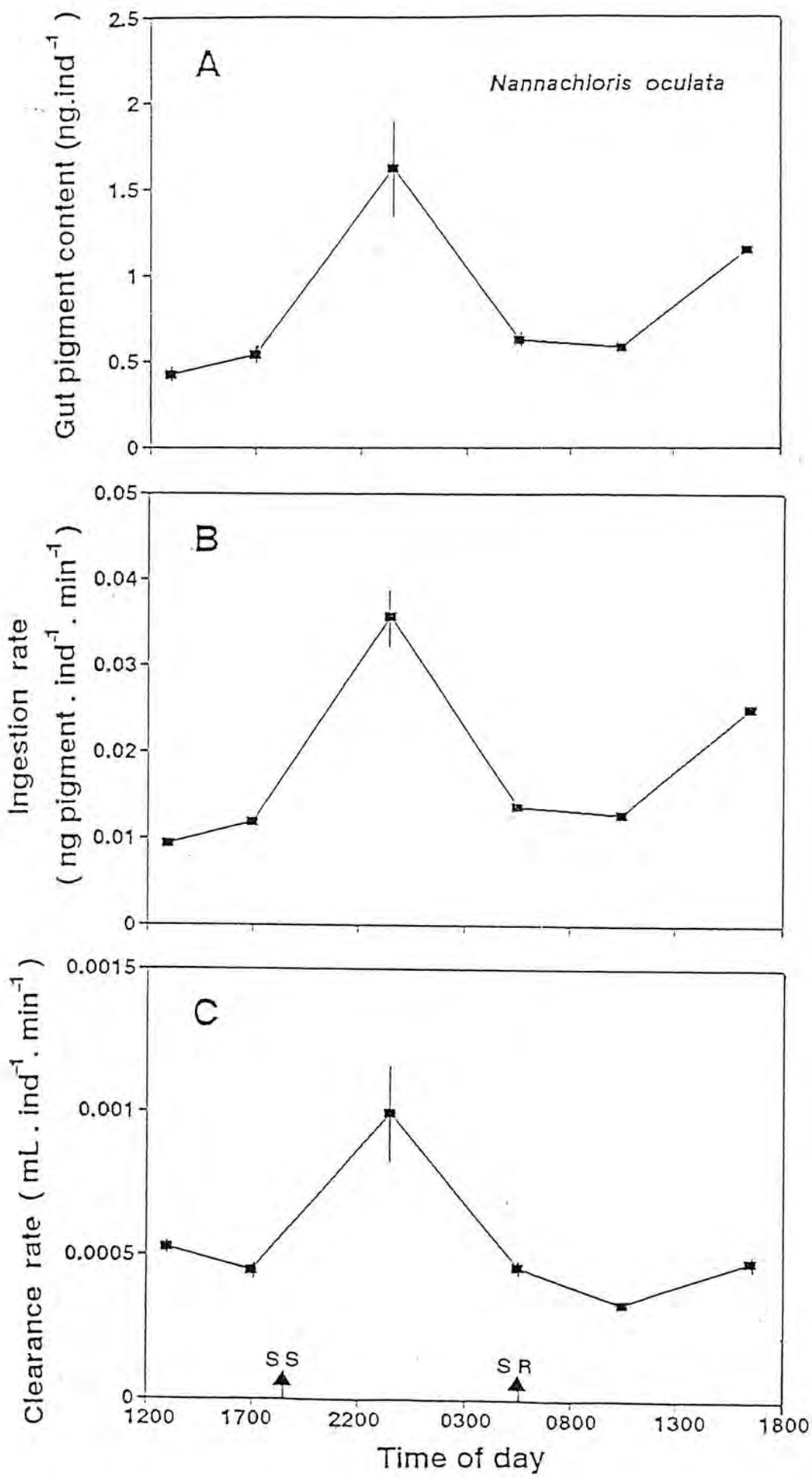

A
Chaetoceros gracilis
Gut pigment content (ng.ind^{-1})
2
1.5
1
0.5
0
B
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
0.05
0.04
0.03
0.02
0.01
0
C
Clearance rate (mL . ind^{-1} . min^{-1})
0.0005
0.0004
0.0003
0.0002
0.0001
0
S S
S R
1000
1500
2000
0100
0600
1100
1600
2100
Time of day

Fig. 6.4 Diel variation of gut pigment content (A), ingestion rate (B) and clearance rate (C) for *Penilia avirostris*. Experiment was carried out on July 17 - July 18, 1990. Times of sunset (SS) and sunrise (SR) were 1830 h and 0530 h. Animals fed *Nannachloris oculata* at 30 ng Chl*a*. mL^{-1}. Each point represents the average of 2 fluorometer counts using a total of 40 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.


A
Nannachloris oculata
Gut pigment content (ng.ind-1)
2.5
2
1.5
1
0.5
0
B
Ingestion rate
(ng pigment . ind-1 . min-1)
0.05
0.04
0.03
0.02
0.01
0
C
Clearance rate (mL . ind-1 . min-1)
0.0015
0.001
0.0005
0
SS
SR
1200
1700
2200
0300
0800
1300
1800
Time of day

Similar diel patherns were observed for ingestion rate and clearance evacuation rate.

Grazing performance of *P. avirostris* on different types of algae was evaluated in the laboratory. Because previous studies (Gore 1980; Turner *et al.* 1988) showed that *P. avirostris* prefers small cells to large ones, phytoplankters with cell size < 20 μm were chosen for experiments. To study the feeding response of *P. avirostris* on naturally occurring food particles, algal species isolated from surface water Tolo Harbour were included. Experiments were conducted over a wide range of food concentrations to include the wide range of food levels encountered in Tolo Harbour.

In general, the gut pigment content and ingestion rate of *P. avirostris* increased with food concentrations (Fig. 6.5 - Fig. 6.12). In the case of the small green algae *N. oculata*, *I.* aff. *galbana*, *C. pyrenoidosa* and *C. ellipsoidea*, gut pigment content and ingestion rate continued to increase through the entire range of food concentrations tested. When *C. pyrenoidosa* cells were offered as food, maximum gut content of about 5 ng pigment.ind^{-1} was reached at food concentration of 1800 ng Chl*a*.mL^{-1}. When the green alga *Platymonas* sp. and the diatoms *C. gracilis*, *C. minus* and *S. costatum* were provided as food, gut pigment content and ingestion increased with food concentration to a maximum level, and then began to level off or even decrease slightly with further increases in food concentration. In experments with *S. costatum*, maximum gut content was

Fig. 6.5 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Nannachloris oculata*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

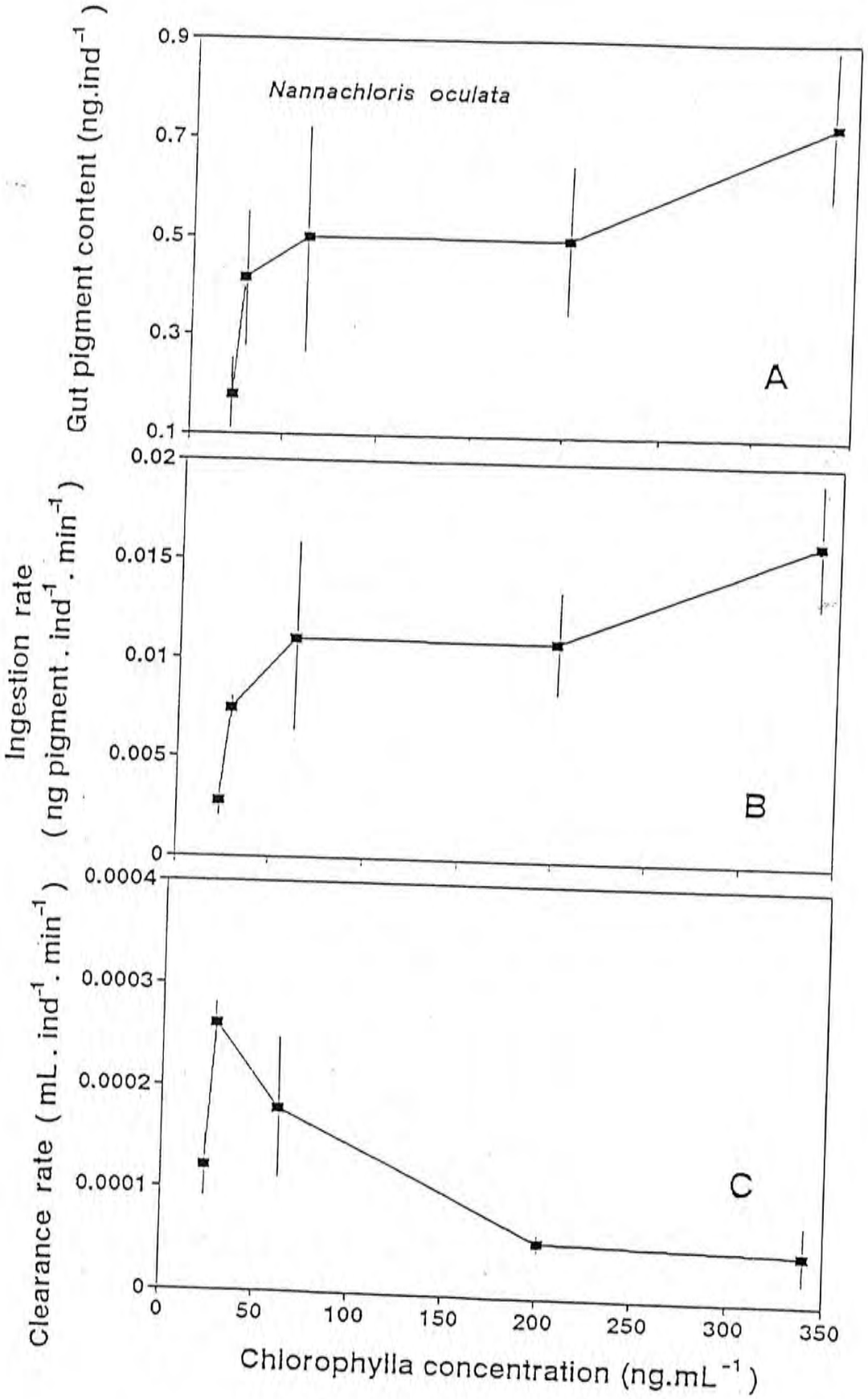

Nannachloris oculata
Gut pigment content (ng.ind^{-1})
0.9
0.7
0.5
0.3
0.1
A
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
0.02
0.015
0.01
0.005
0
B
Clearance rate (mL . ind^{-1} . min^{-1})
0.0004
0.0003
0.0002
0.0001
0
C
0
50
100
150
200
250
300
350
Chlorophylla concentration (ng.mL^{-1})

Fig. 6.6 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Isochrysis* aff. *galbana*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

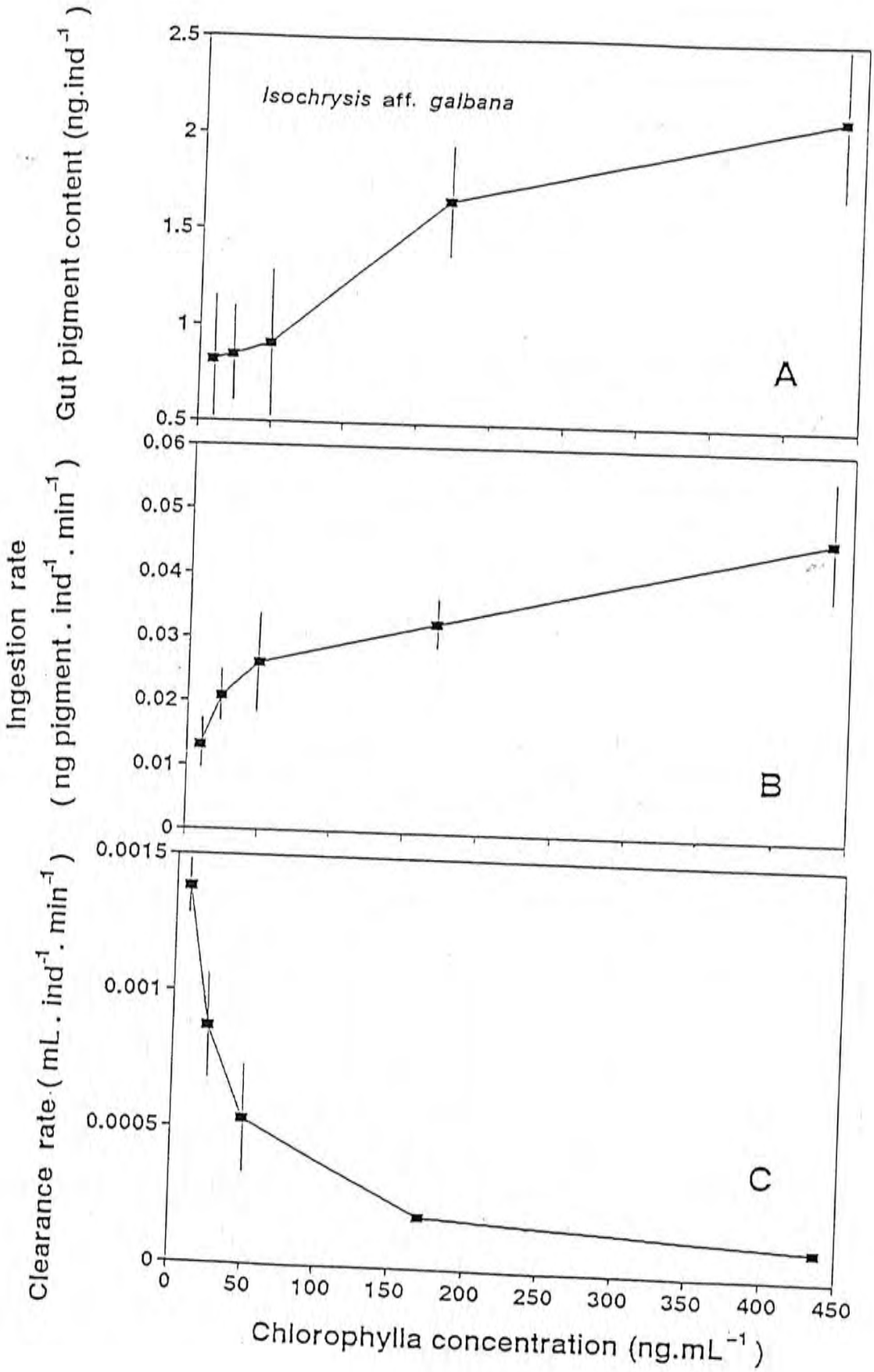

Isochrysis aff. galbana
Gut pigment content (ng.ind-1)
Ingestion rate
(ng pigment . ind-1 . min-1)
Clearance rate (mL . ind-1 . min-1)
A
B
C
2.5
2
1.5
1
0.5
0.06
0.05
0.04
0.03
0.02
0.01
0
0.0015
0.001
0.0005
0
0
50
100
150
200
250
300
350
400
450
Chlorophylla concentration (ng.mL-1)

Fig. 6.7 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Chlorella pyrenoidosa*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

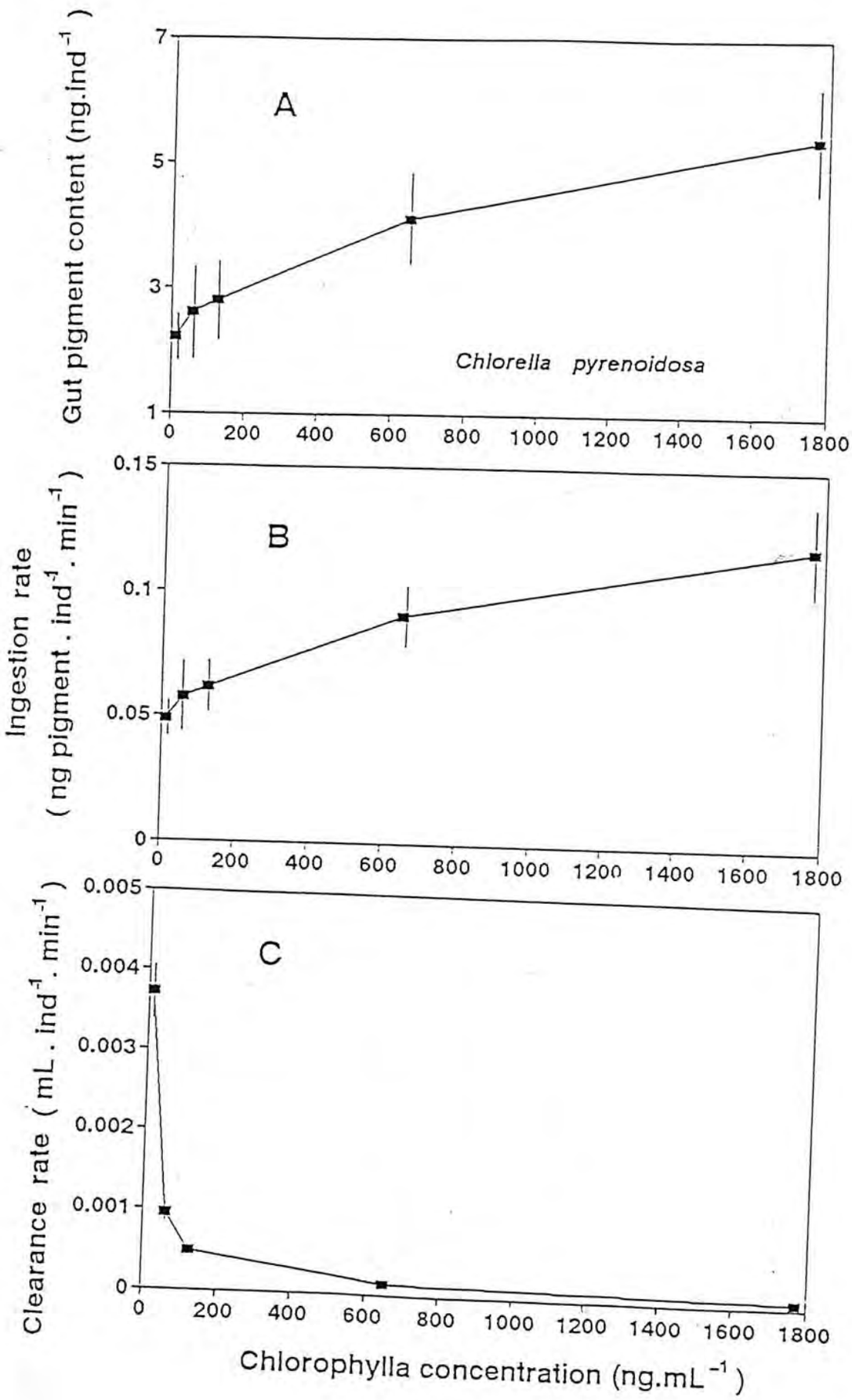

A
Gut pigment content (ng.Ind^{-1})
7
5
3
1
Chlorella pyrenoidosa
0
200
400
600
800
1000
1200
1400
1600
1800
B
Ingestion rate
(ng pigment . ind^{-1}. min^{-1})
0.15
0.1
0.05
0
C
Clearance rate (mL . ind^{-1}. min^{-1})
0.005
0.004
0.003
0.002
0.001
Chlorophylla concentration (ng.mL^{-1})

Fig. 6.8 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Chlorella ellipsoidea*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

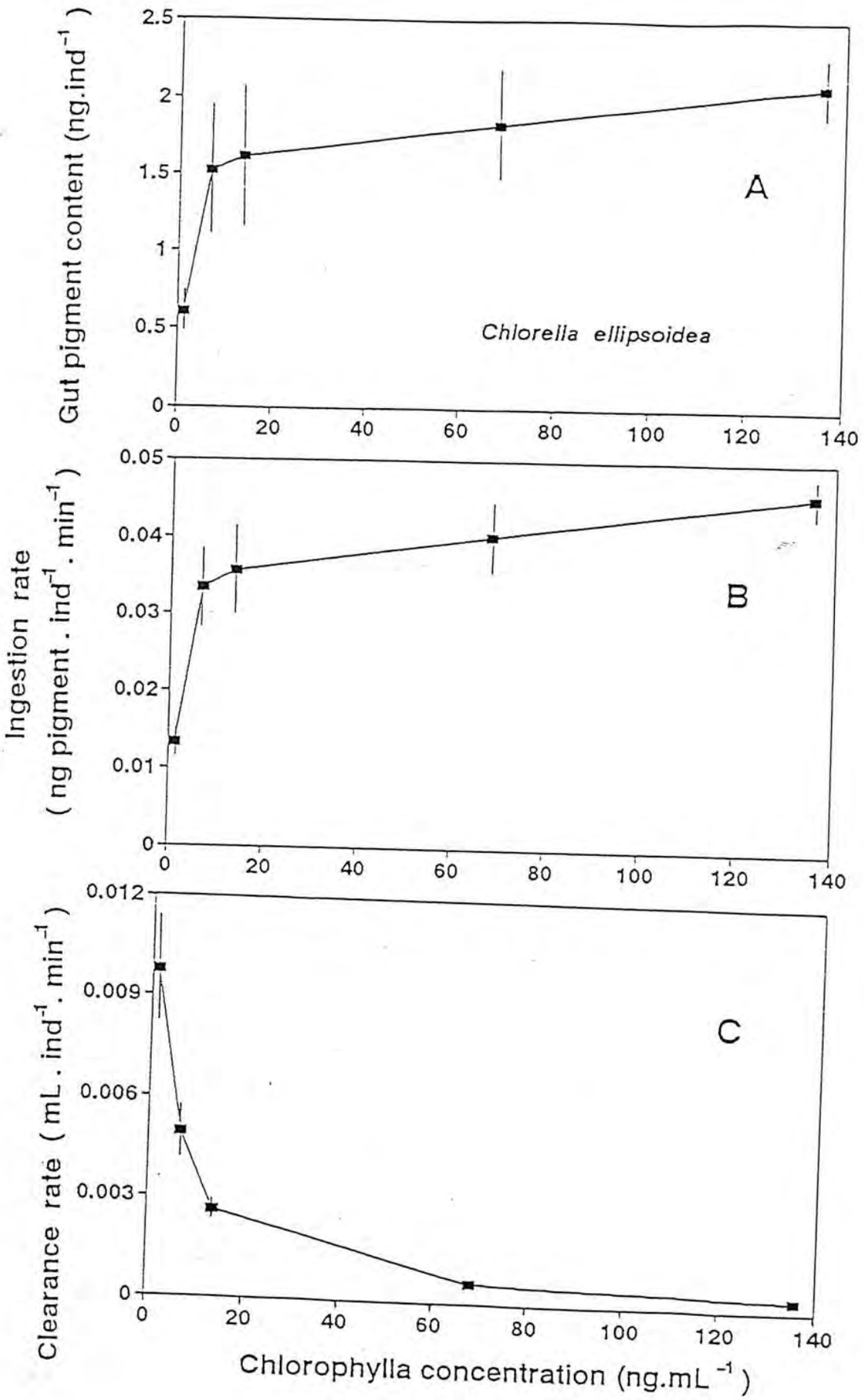

Gut pigment content (ng.ind^{-1})
2.5
2
1.5
1
0.5
0
A
Chlorella ellipsoidea
0
20
40
60
80
100
120
140
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
0.05
0.04
0.03
0.02
0.01
0
B
0
20
40
60
80
100
120
140
Clearance rate (mL . ind^{-1} . min^{-1})
0.012
0.009
0.006
0.003
0
C
0
20
40
60
80
100
120
140
Chlorophylla concentration (ng.mL^{-1})

Fig. 6.9 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Platymonas* sp. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

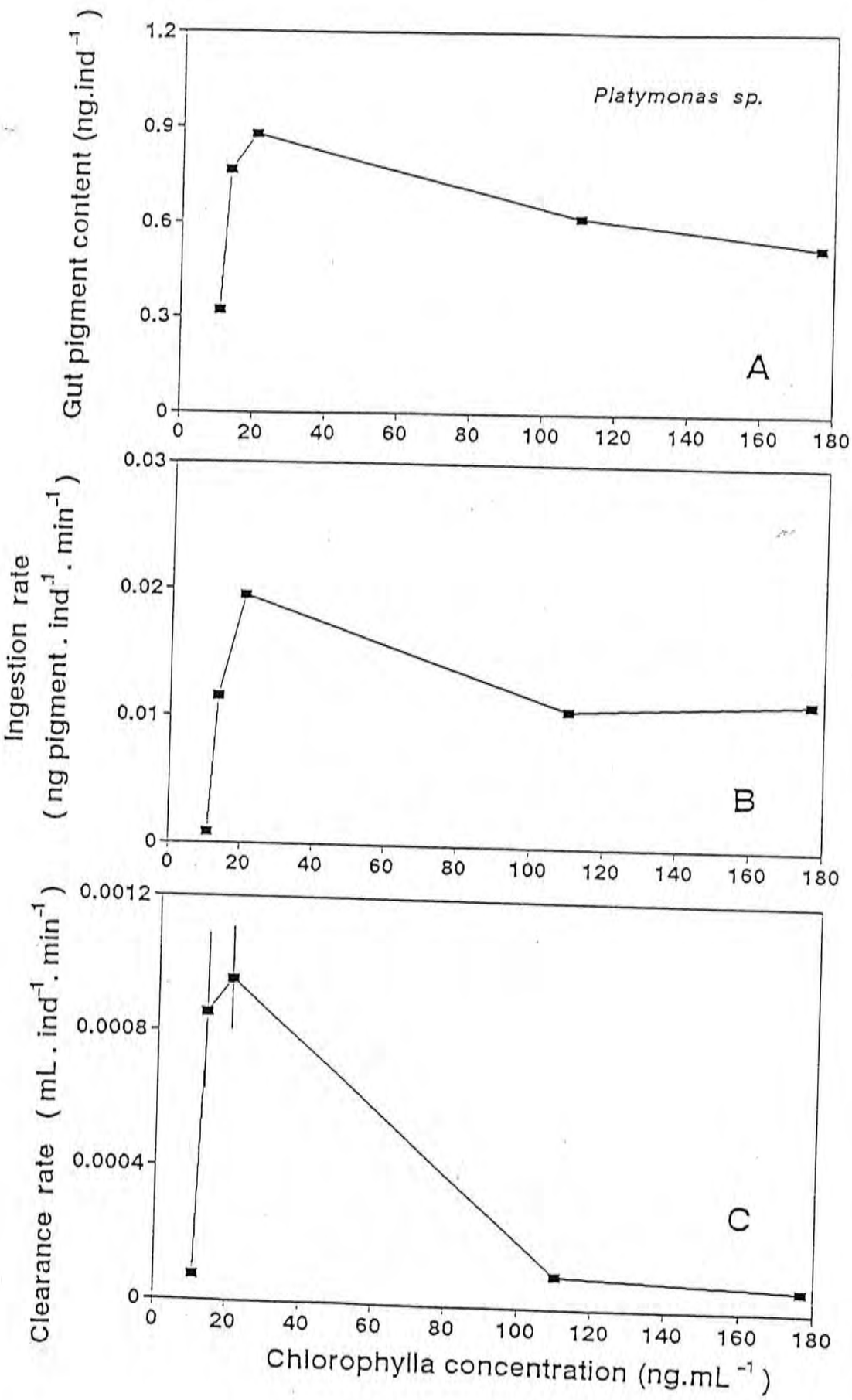

Platymonas sp.
Gut pigment content (ng.ind^{-1})
1.2
0.9
0.6
0.3
0
A
0 20 40 60 80 100 120 140 160 180
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
0.03
0.02
0.01
0
B
0 20 40 60 80 100 120 140 160 180
Clearance rate (mL . ind^{-1} . min^{-1})
0.0012
0.0008
0.0004
0
C
0 20 40 60 80 100 120 140 160 180
Chlorophylla concentration (ng.mL^{-1})

Fig. 6.10 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Chaetoceros gracilis*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

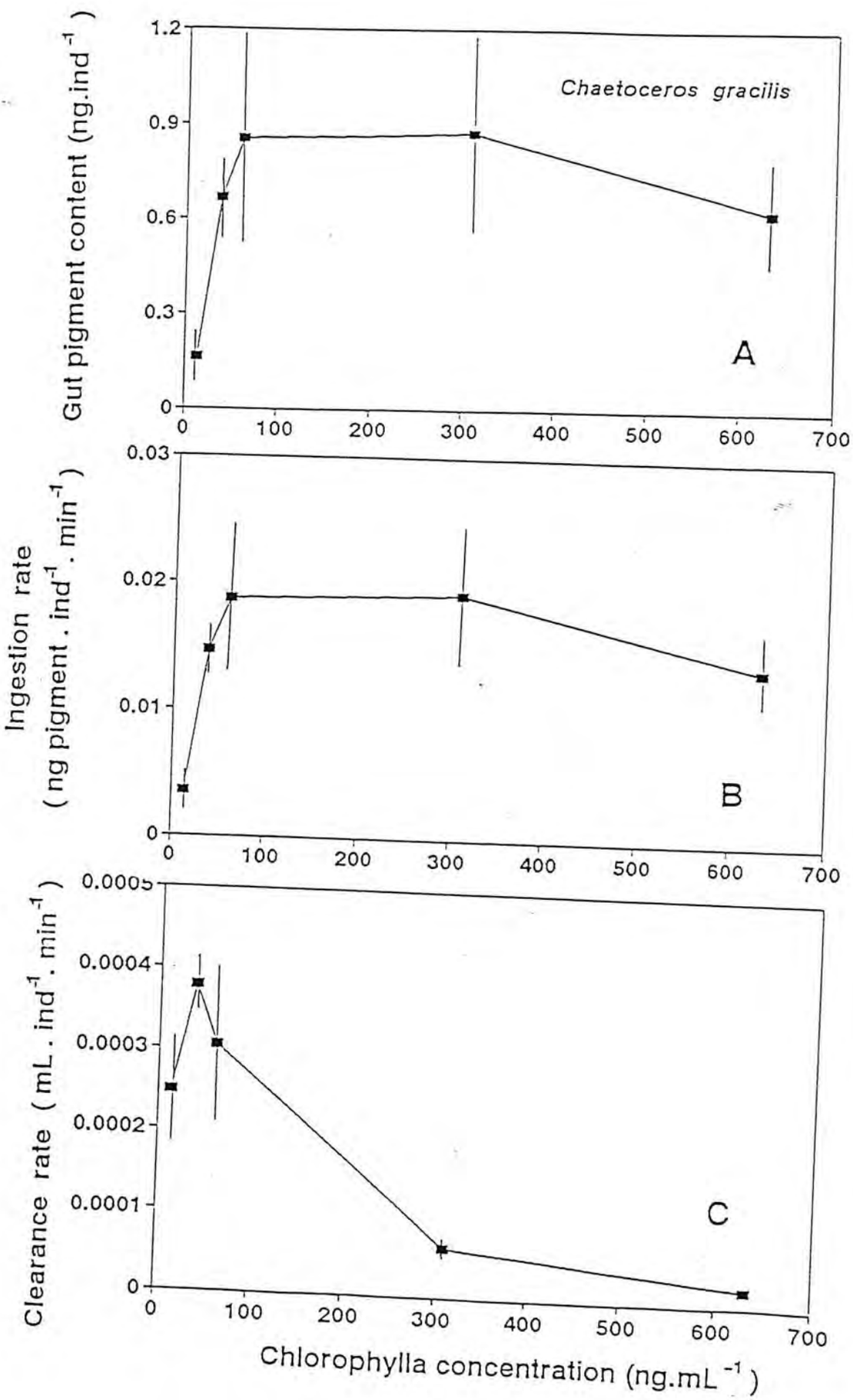

Chaetoceros gracilis
Gut pigment content (ng.ind-1)
1.2
0.9
0.6
0.3
0
A
Ingestion rate
(ng pigment . ind-1 . min-1)
0.03
0.02
0.01
0
B
Clearance rate (mL . ind-1 . min-1)
0.0005
0.0004
0.0003
0.0002
0.0001
0
C
0
100
200
300
400
500
600
700
Chlorophylla concentration (ng.mL-1)

Fig. 6.11 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Chaetoceros minus*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.

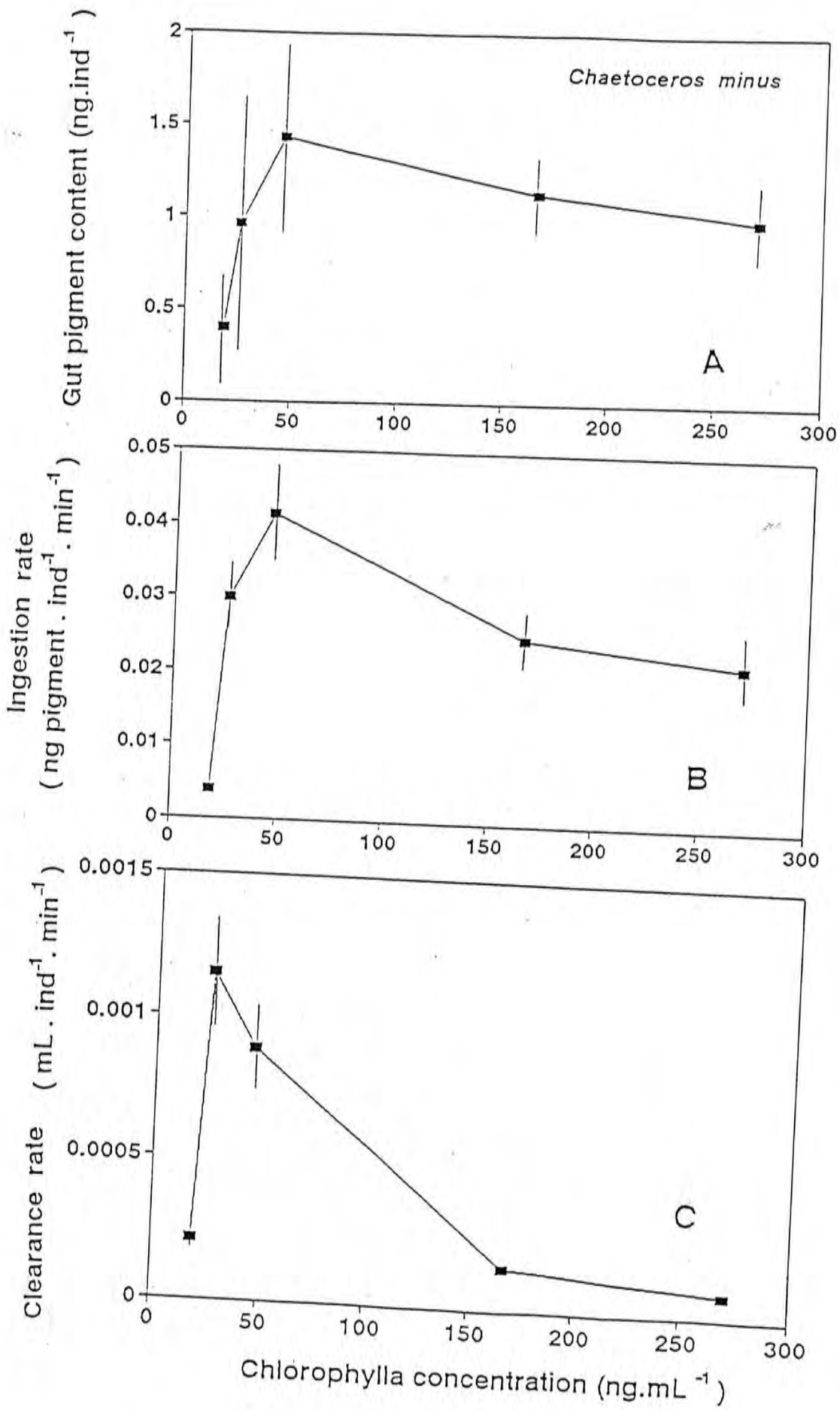
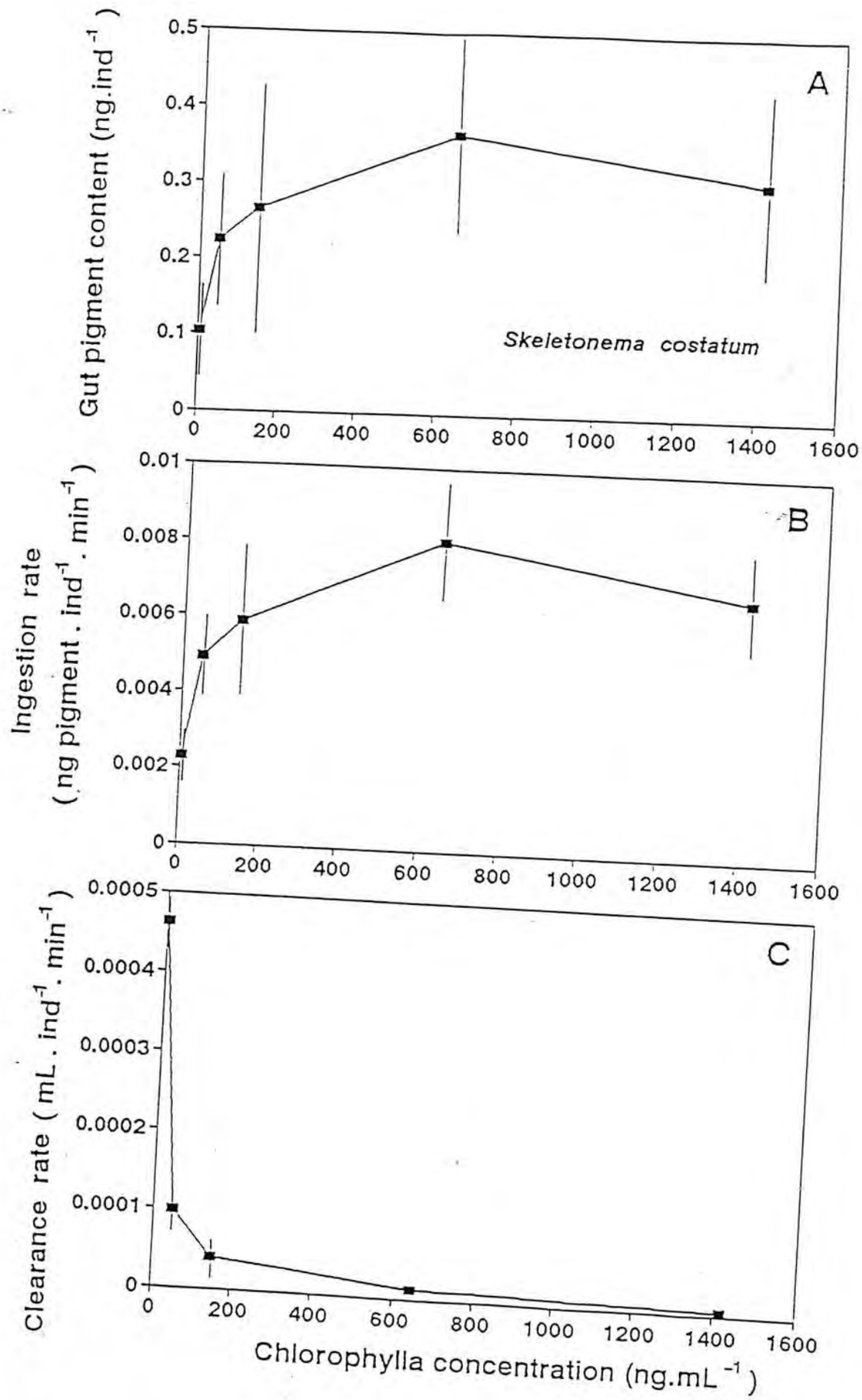

Chaetoceros minus
Gut pigment content (ng.ind-1)
Ingestion rate
(ng pigment . ind-1 . min-1)
Clearance rate (mL . ind-1 . min-1)
Chlorophylla concentration (ng.mL-1)
A
B
C
0
0.5
1
1.5
2
0.01
0.02
0.03
0.04
0.05
0.0005
0.001
0.0015
50
100
150
200
250
300

Fig. 6.12 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* at different concentrations of *Skeletonema costatum*. Each point represents mean of 5 fluorometer counts using a total of 100 animals. Vertical bars represent $\pm$ 1 SD. If no bars are shown, they are within the region of the symbol.


A
Gut pigment content (ng.ind^{-1})
0.5
0.4
0.3
0.2
0.1
0
Skeletonema costatum
0
200
400
600
800
1000
1200
1400
1600
B
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
0.01
0.008
0.006
0.004
0.002
0
C
Clearance rate (mL . ind^{-1} . min^{-1})
0.0005
0.0004
0.0003
0.0002
0.0001
0
Chlorophylla concentration (ng.mL^{-1})

only about 0.35 ng pigment.ind^{-1} at 600 ng Chl*a*.mL^{-1}. This was much lower than the maximum values recorded for the other algae. Similarly, lowest ingestion rates occurred when *P. avirostris* were fed *S. costatum*. Maximum ingestion rate was 0.008 ng pigment.ind^{-1}.min^{-1} at 600 ng Chl*a*.mL^{-1}.

Relationship between clearance rate and food concentration revealed 2 possible strategies in the feeding mechanism of *P. avirostris*. Going from high to low concentrations of *I.* aff. *galbana*, *C. pyrenoidosa*, *C. ellipsoidea* and *S. costatum*, the clearance rate of *P. avirostris* increased exponentially to a maximum when food concentration approached zero. When cells of *N. oculata*, *Platymonas* sp., *C. gracilis* and *C. minus* were offered as food, clearance rate also varied inversely with food concentration. But as food concentrations dropped below a certain level, there was an obvious depression of the clearance rate.

6.3.2. *In situ* study

No clear relationship was found between the abundance of *P. avirostris* and chlorophyll*a* concentration (Fig. 6.13). In the field gut pigment content represents the amount of phytoplankton ingested in the short period of time before the animal was collected. Gut pigment content of *P. avirostris* in Tolo Harbour was measured in June (Fig. 6.14) and November 1989 (Fig. 6.15). In June the maximum level of gut fullness in *P. avirostris* was > 2 ng pigment.ind^{-1}. This was much higher than the

Fig. 6.13 Relationship between *Penilia avirostris* density and chlorophyll*a* concentration in Tolo Harbour.

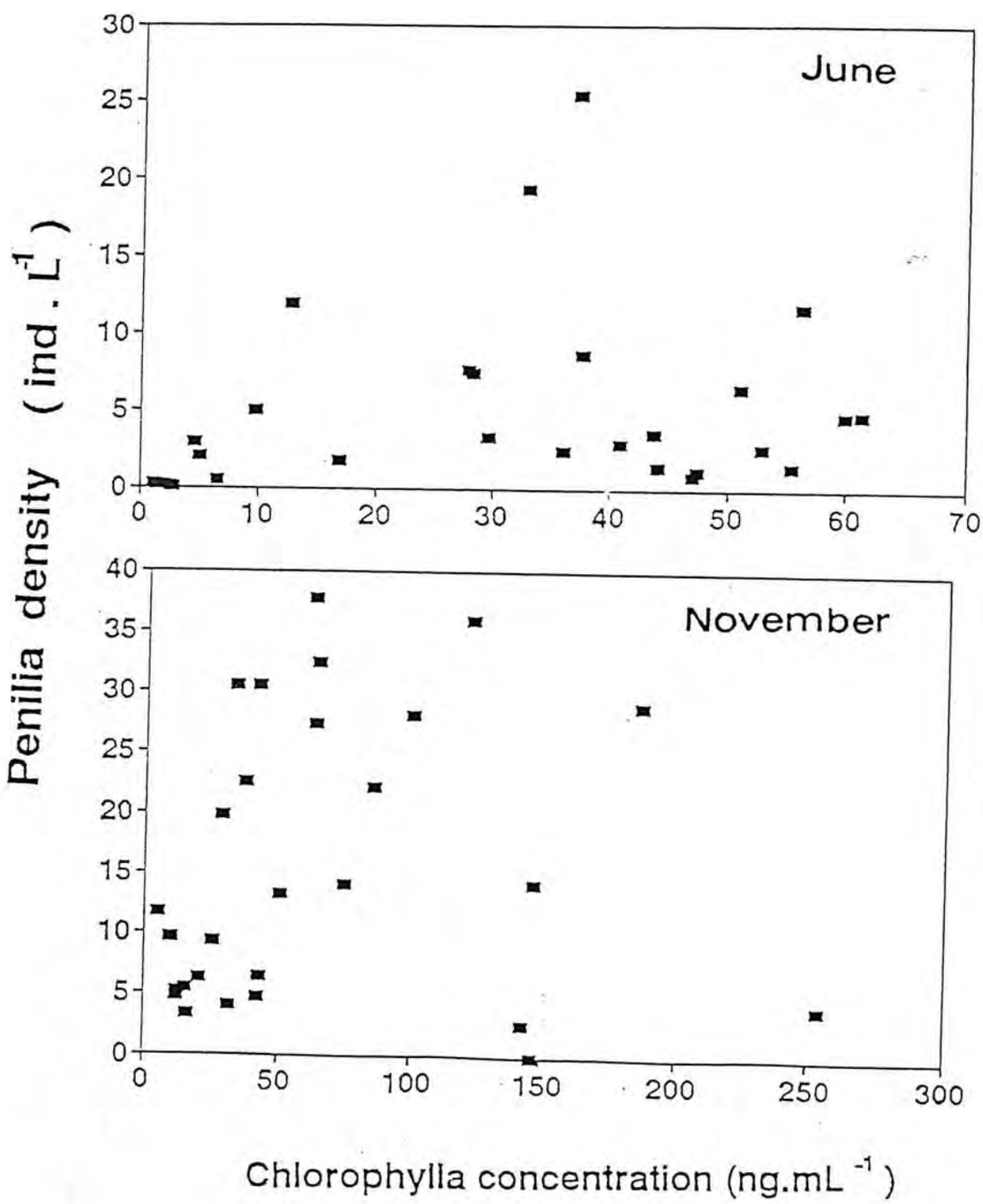

June
November
Penilia density (ind . L-1)
Chlorophylla concentration (ng.mL -1)
0
5
10
15
20
25
30
35
40
50
60
70
100
150
200
250
300

Fig. 6.14 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* in relation to *in situ* food concentration in June, 1989. Each point represents mean of 2 fluorometer counts using a total of 40 animals.

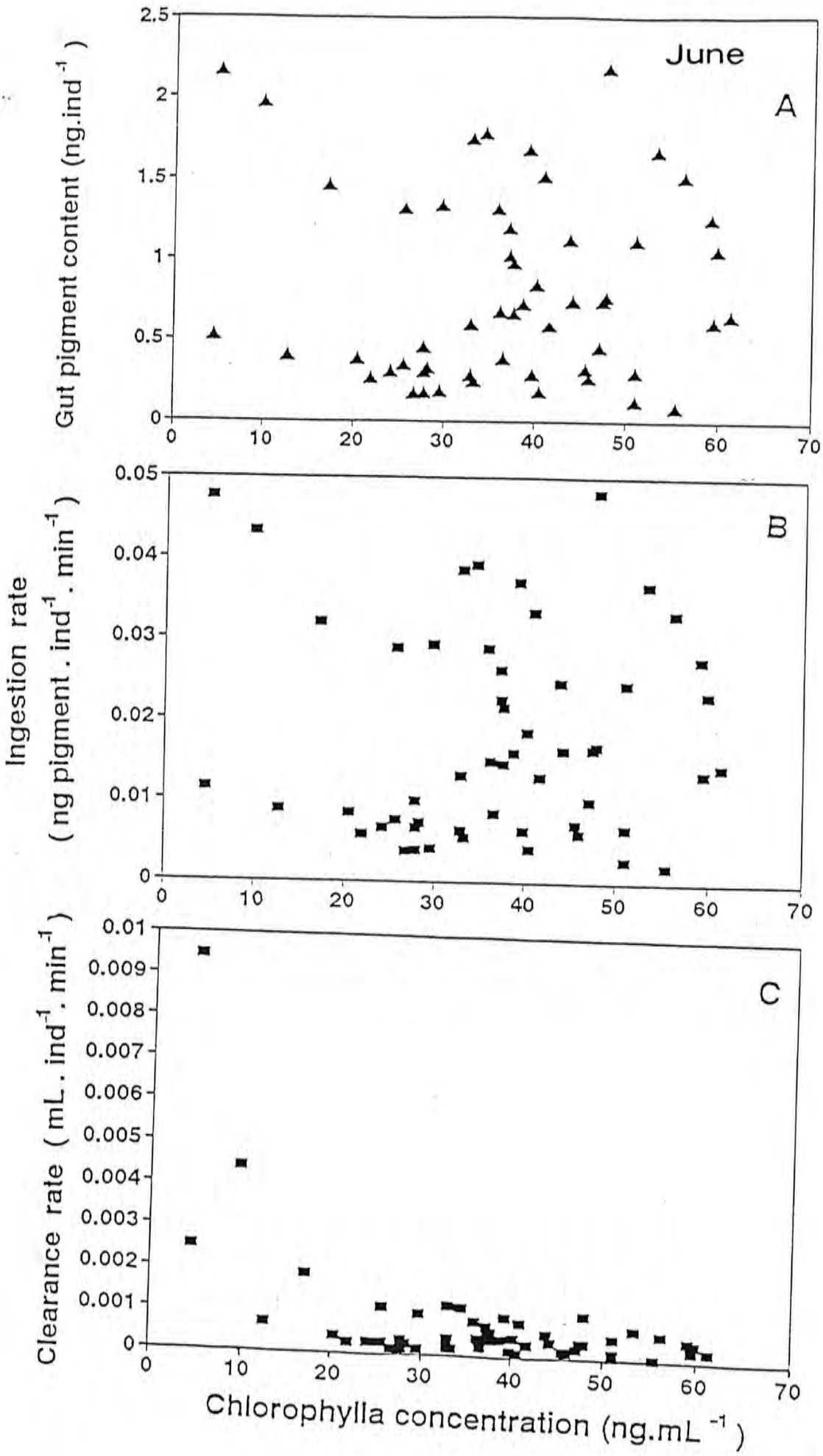
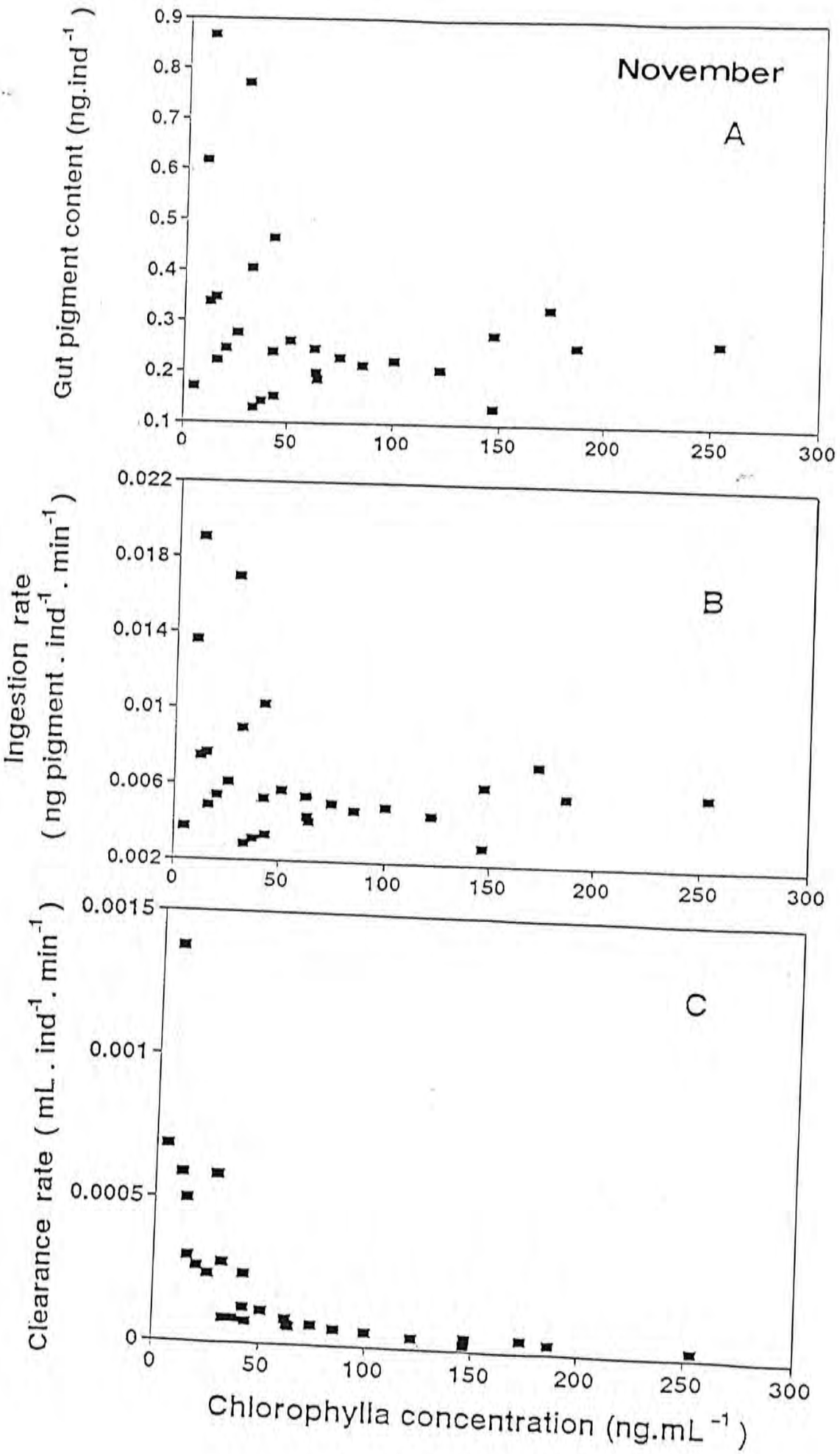

June
A
B
C
Gut pigment content (ng.ind -1)
Ingestion rate
(ng pigment . ind -1 . min -1)
Clearance rate (mL . ind -1 . min -1)
Chlorophylla concentration (ng.mL -1)
2.5
2
1.5
1
0.5
0
0.05
0.04
0.03
0.02
0.01
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
10
20
30
40
50
60
70

Fig. 6.15 Gut pigment content (A), ingestion rate (B) and clearance rate (C) of *Penilia avirostris* in relation to *in situ* food concentration in November, 1989. Each point represents mean of 2 fluorometer counts using a total of 40 animals.


November
A
B
C
Gut pigment content (ng.ind^{-1})
Ingestion rate
(ng pigment . ind^{-1} . min^{-1})
Clearance rate (mL . ind^{-1} . min^{-1})
Chlorophylla concentration (ng.mL^{-1})
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.022
0.018
0.014
0.01
0.006
0.002
0.0015
0.001
0.0005
0
0
50
100
150
200
250
300

maximum level of < 1 ng pigment.ind^{-1} recorded in November even though chlorophyll*a* concentrations were considerably higher in November. In general, gut pigment content in *P. avirostris* did not appear to associate with the concentration of chlorophyll*a* recorded in the location from which the animals were collected. During the red tide bloom in November at least 30 % of the surface area of Tolo Harbour was covered by a shade of red colour. Gut fullness of *P. avirostris* was generally < 0.4 ng pigment.ind^{-1} at locations where chlorophyll*a* concentrations were > 50 ng.mL^{-1}.

Ingestion rates of *P. avirostris* as estimated from the gut content also did not correspond with chlorophyll*a* concentration in the location from which the animals were captured (Figs. 6.14 and 6.15). Maximum ingestion rate in June was around 0.05 ng pigment.ind^{-1}.min^{-1}. In Novermber the maximum ingestion rate was only around 0.02 ng.pigment.ind^{-1}.min^{-1}. Even lower values were recorded at locations where chlorophyll*a* level was >50 ng.mL-1. On both dates, a negative exponential relationship was found between clearance rate and chlorophyll*a* concentration.

Tables 6.1 and 6.2 showed the feeding impact of *P. avirostris* in Tolo Harbour during June and November 1989. The relationship between the feeding impact of *P. avirostris* and chlorophyll*a* concentration in the field is presented in Fig. 6.16. While the highest value recorded in June was 31.56 mL swept clear.L^{-1}.day^{-1}, values at all sampling locations was < 20 mL

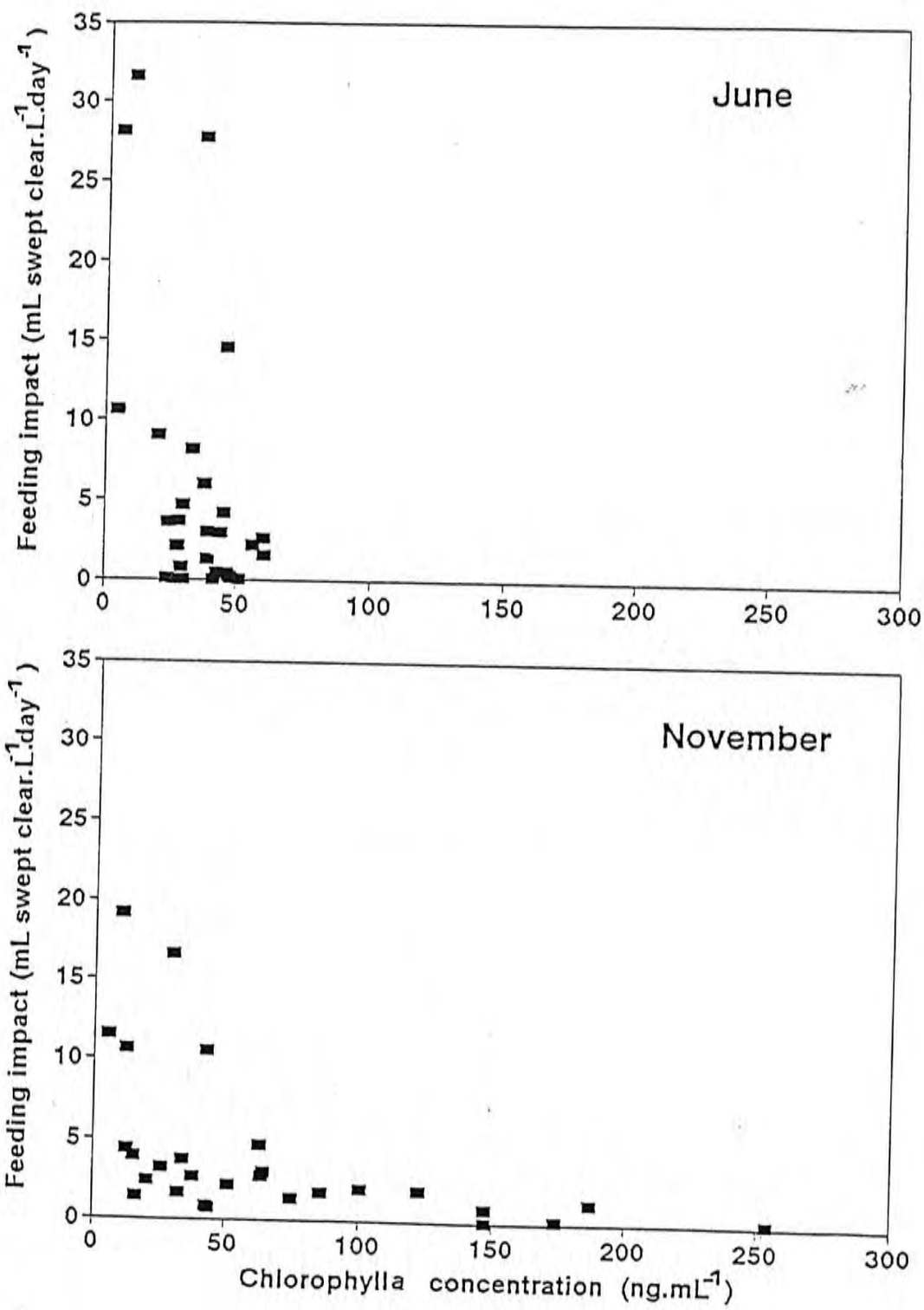
Table 6.1 Feeding impact of *Penilia avirostris* in Tolo Harbour during June, 1989.

Station	Density of *P.avirostris* (ind.L^{-1})	Chlorophyll*a* concentration (ng.mL^{-1})	Clearance rate (mL.ind^{-1}.day^{-1})	Feeding impact (mL swept clear.L^{-1}.day^{-1})
1	2.93	4.56	3.62	10.63
2	0.16	41.25	0.26	0.04
3	2.07	5.04	13.61	28.15
4	4.96	9.78	6.36	31.56
5	3.28	29.64	1.42	4.67
6	0.06	51.10	0.13	0.01
7	0.20	29.93	0.22	0.04
8	11.95	20.22	0.76	9.06
9	0.24	23.73	0.40	0.10
10	0.14	26.83	0.30	0.04
11	0.08	47.82	0.98	0.08
12	7.48	24.31	0.48	3.59
13	25.46	36.46	1.09	27.74
14	1.80	28.12	2.03	3.67
15	7.68	27.81	0.27	2.08
16	0.48	29.20	1.66	0.80
17	11.71	45.26	1.25	14.60
18	8.63	37.60	0.69	5.98
19	19.34	32.85	0.42	8.20
20	2.93	39.05	1.02	3.00
21	6.54	44.90	0.64	4.20
22	4.68	59.86	0.56	2.61
23	4.75	60.41	0.33	1.57
24	3.57	43.80	0.81	2.89
25	2.63	56.21	0.83	2.18
26	1.44	47.63	0.14	0.20
27	2.44	38.87	0.52	1.27
28	0.81	43.62	0.49	0.39
29	1.46	42.34	0.34	0.49
30	1.14	46.54	0.36	0.41

Table 6.2 Feeding impact of *Penilia avirostris* in Tolo Harbour during November, 1989.

Station	Density of *P.avirostris* ($ind.L^{-1}$)	Chlorophyll*a* concentration ($ng.mL^{-1}$)	Clearance rate ($mL.ind^{-1}.day^{-1}$)	Feeding impact (mL swept clear.$L^{-1}.day^{-1}$)
1	11.67	5.48	0.98	11.49
2	6.34	20.60	0.38	2.40
3	4.75	42.61	0.18	0.84
4	0.01	146.85	0.03	0.00
5	-------	-------	-------	-------
6	3.28	16.34	0.43	1.41
7	5.49	15.43	0.71	3.93
8	9.69	9.89	1.98	19.17
9	5.17	12.67	0.85	4.38
10	4.75	12.28	2.23	10.62
11	19.81	29.13	0.84	16.62
12	9.38	25.68	0.34	3.21
13	4.11	32.18	0.40	1.64
14	30.53	42.43	0.35	10.60
15	6.47	43.65	0.11	0.71
16	22.51	37.56	0.12	2.68
17	30.56	33.60	0.12	3.72
18	32.37	64.27	0.09	2.95
19	27.31	63.51	0.10	2.70
20	37.69	62.78	0.12	4.68
21	22.07	85.78	0.08	1.75
22	13.24	51.10	0.16	2.14
23	14.00	74.82	0.10	1.36
24	28.14	100.37	0.07	1.99
25	35.91	122.27	0.05	1.91
26	28.91	186.76	0.04	1.25
27	2.65	173.56	0.06	0.16
28	-------	-------	-------	-------
29	4.07	253.75	0.03	0.13
30	14.20	147.10	0.06	0.85

Fig. 6.16 Relationship between the feeding impact of *Penilia avirostris* and chlorophyll*a* concentration in Tolo Harbour.


June
November
Feeding impact (mL swept clear.L-1.day-1)
Chlorophylla concentration (ng.mL-1)
0
5
10
15
20
25
30
35
0
50
100
150
200
250
300

swept clear.L^{-1}.day^{-1} during November. During the red tide occurrence in November, grazing impact of *P. avirostris* in locations with chlorophyll*a* concentration > 50 ng.mL^{-1} was usually lower than 5 mL swept clear.L^{-1}.day^{-1}.

6.4. Discussion

In this study, feeding rates of *Penilia avirostris* were measured using the gut fluorescence technique. The occurrence of pigment destruction in the gut presents a major possibility of underestimation in feeding rate measurements (Conover *et al.* 1986; Wang and Conover 1986; Pasternak and Drits 1988). However, some authors have reported close agreement between feeding rates determined by gut fluorescence method and other direct measurements (Dagg and Grill 1980; Kiorboe *et al.* 1985; Peterson *et al.* 1990). In general, clearance values obtained in the present study are within the range of those reported by Paffenhöfer and Orcutt (1986).

Diel variations in feeding have been observed in many zooplankton species (Mackas and Bohrer 1976; Peterson *et al.* 1990). In this study, diel variations in feeding behaviour of *P. avirostris* fed *C. gracilis* and *N. oculata* was observed in 24-h feeding experiments. Gut pigment content began to increase around sunset and reached a maximum about 3 times greater than mean daytime values. Maximum amount of pigment in the guts of *P. avirostris* during nightime was around 1.5 ng.ind^{-1}. For animals fed *C. gracilis*, gut pigment content began to decline after midnight and dropped to about daytime level shortly before sunrise. *P. avirostris* fed *N. oculata* were not sampled for gut pigment content analysis just before sunrise, but individuals sampled shortly after sunrise at 0600 h averaged only about 0.6 ng pigment.ind^{-1}. These results suggest that gut pigment content in *P. avirostris* was highest around midnight, and then returned to daytime values before sunrise, at 0530 h.

Diel variations in feeding among marine zooplankton have often been associated with diel vertical migration. Gauld (1952) showed that diel changes in gut content of the calanoid copepod *Calanus finmarchicus* were the result of animals migrating into and out of the food- rich layer in the surface. On the other hand, Petipa (1958) argued that there is a diel feeding periodicity in addition to vertical migration. Subsequently, several investigators (Nicolajsen *et al.* 1983; Head *et al.* 1985) reported diel feeding periodicity in non-migrating copepods, while Haney and Hall (1973) found no diel change in the filtering rate of the freshwater copepod *Diaptomus pallidus*, despite a pronounced vertical migration. Peterson *et al.* (1990) regarded diel feeding variations in species that do not perform diel vertical migration as diel feeding rhythm. While many investigators (Head *et al.* 1985; Stearns 1986; Peterson *et al.* 1990) agree that diel feeding rhythms are controlled by incipient light intensity, results in this study reveal that the gut content of *P. avirostris* started to decline before sunrise.

P. avirostris kept in 1000 L outdoor tanks showed marked diel periodicities in gut pigment contents. The vertical distribution pattern of *P. avirostris* in the experimental tanks were not monitored. However, because algae were distributed evenly in the experimental tanks, the animals were exposed to food regardless of their vertical position in the water column. The observed feeding periodicities, therefore, cannot be adequately explained by Gauld's hypothesis. Since *P. avirostris* exposed to food during daytime still reduced their feeding intensity markedly after

sunset, the result support Petipa's hypothesis of a diel feeding rhythm which is not related to vertical migration.

P. avirostris and many other marine cladocerans are restricted to the surface during daytime (Onbé 1977) and, as a result, exposed to food during daylight hours. The adaptive significance of diel feeding rhythms in zooplankters which do not migrate vertically is unclear (Nicolajsen *et al.* 1983). McAllister (1970) suggested that diel feeding could benefit zooplankters that concentrate their feeding in the early evening to utilize maximum amount of photosynthetically fixed energy before appreciable phytoplankton respiration has occurred.

Although marine cladocerans are mostly commonly found in the coastal waters of warm temperate regions (Bosch and Taylor 1973, Onbé 1977), little is known about their distribution in relation to their feeding ecology. Recently, Paffenhöfer and Orcutt (1986) reported that *P. avirostris* are well adapted to the low food levels of oligotrophic open oceanic waters and may play an important role in trophodynamic pathways of oligotrophic oceanic waters, as well as eutrophicated neritic waters.

Considering the frequent association of *P. avirostris* with relatively productive waters, Paffenhöfer and Orcutt (1986) were surprised to note that survivorship and fertility of *P. avirostris* fed *Isochrysis* aff. *galbana* (4.5 µm diameter) were highest at the relatively low food concentration of 0.72 ng Chl*a*.mL^{-1}. They proposed that their observation can probably be explained by the fact that *P. avirostris* prefers particles < 15 µm and its

feeding mechanisms were inhibited by an over abundance of small particles. In eutrophic waters, where most particles are > 15 μm, Paffenhöfer and Orcutt (1986) hypothesized that *P. avirostris* can utilize the small particles without interruption. In Tolo Harbour the phytoplankton is dominated by cells > 30 μm in diameter (personal observation). During red tide occurrence almost all chlorophyll*a* consists of large particles (> 100 μm) which were not easily ingested by *P. avirostris*. Field observations in November 1989 revealed that feeding intensity of *P. avirostris* was greatly reduced during red tide occurrence. Because incipient chlorophyll*a* concentration does not reflect the actual amount of edible food available to *P. avirostris* in the eutrophic waters of Tolo Harbour, no relationship was found between the level of chlorophyll*a* in the water and the feeding intensity of *P. avirostris*. However, it must be noted that the low feeding intensity measured in *P. avirostris* could be the result of daytime sampling.

When *P. avirostris* were fed small cells such as *Isochrysis* aff. *glbana* (5 μm), *Nannachloris oculate* (5 μm), *Chlorella ellipsoidea* (5 μm) and *Chlorella pyrenoidosa* (5 μm), their ingestion rate increased with food concentration. In contrast, when animals were given larger particles such as the diatoms *Chaetoceros gracilis* (7 μm), *C. minus* (8 μm) and *Skeletonema costatum* (10 μm), and the larger flagellate *Platymonas* sp. (20 μm), their ingestion rate initially increased with food concentration, and then began to either levelled off or decreases slightly at the high food concentrations. These results suggest that the feeding mechanisms of *P. avirostris* were inhibited by an over abundance of particles larger than 5 μm diameter. In

addition, these results are consistent with the finding of Pavlova (1964) that *P. avirostris* only feed on particles with size less then 8 μm diameter, but differ with the observation of Lochhead (1936) and Paffenhöffer and Orcutt (1986) that *P. avirostris* can avoid interruption of feeding activity by large particles. Low ingeston rate and clearance rate in experiments with the chain-forming diatoms *S. costatum*, *C. gracilis* and *C. minus* indicate that chain-forming diatoms may not be suitable *P. avirostris*. Other investigators have demonstrated that filamentous algae have an inhibitory effect on the feeding activity of cladocerans (Webster and Peters 1978). Lam and Ho (1989) reported that *S. costatum* constitutes a large proportion of the total diatom population in Tolo Harbour throughout the year. Welch (1968) pointed out that a high abundance of *S. costatum* is indicative of eutrophication. In Tolo Harbour, *S. costatum* may cause discolouration of seawater and is considered to be an important red tide species (E.P.D. 1990). Low feeding rate of *P. avirostris* on *S. costatum* and other dinoflagellates and their diel rhythm may explain the low ingestion rate and clearance rate recorded in *in situ* experiments.

Some interesting trends were detected in the grazing impact of *P. avirostris* on the phytoplankton in Tolo Harbour. The grazing impact of *P. avirostris* did not increase with increasing chlorophyll*a* concentration in the water. In general, grazing by *P. avirostris* has a minor impact on the phytoplankton of Tolo harbour. Highest recorded impact of 31.6 mL swept clear.L^{-1}.day^{-1} was recorded in June. During the red tide bloom in Novermber, grazing impact by *P. avirostris* was much lower, with highest recorded value at only 19.2 mL swept clear .L^{-1}.day^{-1}. In stations with

chlorophyll*a* concentration > 50 ng.mL^{-1}, grazing impact of *P. avirostris* on the marine phytoplankton was < 5 mL swept clear.L^{-1}.day^{-1}. As mentioned earlier, a very high proportion of the chlorophyll*a* in Tolo Harbour is derived from particles > 30 μm diameter. *Notiluca scintillans*, the major causative species in the red tide occurrence in November 1989, has a diameter >100 μm. Because these large particles are not removed by *P. avirostris*, increase in chlorophyll*a* concentration in the sea would not lead to higher feeding efficiency by the cladocerans.

Chapter 7

General conclusion

Tolo Harbour receives a large amount of nutrients from direct sewage discharges and surface run-off carrying domestic, livestock and industrial wastes. Excessive amount of nutrients are accumulated in the bottom waters and sediments, leading to eutrophication of the water column and development of anoxic conditions in the bottom layer. The consequence of eutrophication was particularly serious in the inner regions of the harbour.

Over recent years, the phytoplankton biomass in Tolo Harbour has increased substantially. In addition, there is a gradual reduction in taxonomic diversity and increased domination by dinoflagellates. Increase in dinoflagellate population has resulted in increased occurrence of red tides has significant impacts, which in turn on the zooplankton community.

Zooplankton abundance in Tolo Harbour exhibits a landward increase from the outer harbour to the inner harbour. At the same time, the density of phytoplankton was lowest in the channel and increased towards the inner harbour. Accumulation of phytoplankton and zooplankton in the inner harbour is likely the result of currents. Increased phytoplankton production is expected eventually to give rise to higher zooplankton abundance, but no correlation is found between chlorophyll*a* concentration and zooplankton abundance. One explanation is that much of the increase in chlorophyll*a* concentrations in Tolo Harbour can be attributed to a dramatic rise in the abundance of dinoflagellates which are inedible for many

herbivorous zooplankton (Huntley *et al.* 1986). The marked decline in population densities of both copepods and cladocerans during 1989 may be related to the increase dominance of dinoflagellates in phytoplankton.

The most important components of the marine zooplankton in Tolo Harbour in terms of number are copepods and cladocerans. Copepods constitute an average of more than 90% of the crustacean zooplankton. Percentage composition of cyclopoid copepods in the total zooplankton increases from 58.4% in the channel to 72% in the inner harbour. The most dominant genera are *Oithona* and *Corycaeus*. The 3 most common calanoid copepods in Tolo Harbour are *Paracalanus, Acartia* and *Temora*. Two genera of cladocerans, *Penilia* and *Evadne*, are also commonly found. Cladocerans make up less than 10% of the crustacean zooplankton. No obvious seasonal trends are observed in the population density of the various zooplankton groups. *Oithona* dominates the copepod population at all areas of Tolo Harbour and appears to be abundant throughout the year. *Coryceaus* remains at a low level at all times except for a brief peak in February 1988. Highest numbers of *Paracalanus, Acartia* and *Temora* are found in summer and autumn. The two genera of cladocerans, *Penilia* and *Evadne*, show no seasonal patterns of occurrence. Their population density is characterized by a series of pulses. The abundance of all major genera declined after January 1989 apparently reflecting the alarming situation of continual deterioration of water quality in Tolo Harbour.

Observations on the biology of zooplankton provides information on factors that control their seasonal dynamics.

The biology and ecology of the cladoceran, *Penilia avirostris*, was studied in detail. Density of *P. avirostris* increases and decreases very rapidly, and the population cycle is not related to water temperature. In general, brood size of *P. avirostris* is low when population density is high. Variation in brood size appears to reflect changes in food availability, with low density spring populations having a large mean brood size and temporarily high density summer populations exhibiting a much lower rate of egg production. Similarly, reduction of mean body length during the summer may also be the result of food limitation.

Association of *P. avirostris* with polluted bays and estuaries (Kiortsis and Moraitou-Apostolopoulou 1975; Grahame 1976; Moore and Sander 1979) and with relatively productive nearshore waters suggests that *P. avirostris* may often be food-limited in the open sea. Results on the food and feeding habits provide further evidence that *P. avirostris* may be food limited in Tolo Harbour. Ingestion rates and clearance rates are low during red tide occurrence. Moreover, no significant correlation is found between *P. avirostris* abundance and chlorophyll*a* concentration in the water. *P. avirostris* exhibits clear diel grazing rhythm in the large outdoor tanks, and feeding rates are clearly affected by food concentration and food type. Ingestion rates of *P. avirostris* are proportional to food concentration below a critical level, and small cells are preferred over large and filamentous algae. However, this phenomenon is not observed in the field. No

relationship is found between ingestion rate and chlorophyll*a* concentration in the location from which the animals are captured. In summary, microphytoplankton (<20 μm) appears to be the most important food organisms for *P. avirostris*, and the impact of *P. avirostris* on the grazing of red tide occurrance is very low.

Finally, results of this study suggests that eutrophication has impacted the marine plankton in Tolo Harbour. The community structure of the phytoplankton plays a role in the determining the population dynamics of the zooplankton. Further studies on the biology of marine zooplankton, especially reproductive biology and feeding ecology, are important for a better understanding of the ecological roles and the dynamics of marine zooplankton communities in Tolo Harbour.

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